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THE INTRA-OCULAR COLOUR-FILTERS OF VERTEBRATES*

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Introduction

Since the discovery of the coloured oil-droplets in the retinal cones of vertebrates by Valentin, and of their widespread distribution by Hannover (1840, 1843), a voluminous literature of interpretation has grown up about these structures. At the present time there is no general agreement as to their rôle in the physiological optics of their possessors. It is our purpose in the present paper to relate to the oil-droplets a number of facts, some long but little known, and others recently discovered, concerning the distribution, nature, and probable functions of several additional

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types of natural intra-ocular colour-filters. These various devices are quite strictly limited to vertebrate forms of similarly circumscribed visual habits. They are almost completely mutually exclusive; only one of these types is ordinarily present in a given animal or group, and none is found in any of the forms which possess oil-droplets. The difficulty of formulating a teleological interpretation of the oil-droplet mosaic is immensely lessened by the consideration of the other, less well known and at first thought simpler types of intra-ocular filters. We believe that as the facts are set forth, the first suspicion of the reader—that all of these apparently so dissimilar types of filters actually serve a common purpose—will become as firm a conviction in his mind as it is in ours.

We have omitted a complete survey of the literature of this field; it is almost wholly devoted to the oil-droplets, and many of the contributions are rendered meaningless, from our standpoint, by a few critical researches to which we shall refer. But little descriptive work has been done upon the oil-droplets in recent years, and the reader will get an adequate conception of the oil-droplet as a structure from such works as Greeff (1900), Garten (1907), Hess (1912), Pütter (1912), and Franz (1913).

We shall content ourselves with a fair statement of each of the theories which have been advanced in explanation of the oil-droplet type of filter, and shall attempt to formulate an explanation in common terms of the entire assemblage of filter types.

Dr. John F. Shepard of the Department of Psychology of the University of Michigan furnished valuable advice on frequent occasions and kindly consented to read and criticise the completed manuscript. We are also very heavily indebted for advice, material, and for the conduction of experiments upon forms not available in our locality, to many members of the above and other institutions; among them: Dr. C. L. Hubbs, Professor T. L. Hankinson, Dr. J. R. Greeley, Mrs. H. T. Gaige, Mr. L. M. Klauber, Professor S. H. Gage, Mr. Werner Schröder, Dr. J. Van Tyne, Miss F. N. Clark, Dr. C. P. Russell, Dr. L. R. Dice, Dr. Leigh Anderson, Dr. R. A. Sawyer, Dr. F. B. Fralick, Dr. Harvey de Bruine, Mr. S. N. Jones, Dr. H. B. Lewis, Dr. L. S. Palmer, Dr. H. G. Houghton, Dr. Brian O'Brien, Dr. W. H. Feldman, Dr. G. F. Laidlaw, Dr. H. W. Feldman, Mr. L. M. Wing, Mr. Laurance Radford, Mr. M. T. Lawton, Mr. F. H. Edmonds, Mr. H. Thornton Rutter, Dr. Walter R. Stokes, Dr. Ludwig Plate, Dr. Viktor Franz, Dr. P. L. Risley, Dr. W. P. Gowland and Dr. Glover M. Allen.

Types of Filters and their Distribution

OIL-DROPLETS.

The oil-droplet filter is usually a single large spheroid, occasionally smaller and multiple, in the choroidal end of the inner segment of the receptor for sharp, photopic vision, the "cone." It is ordinarily coloured rather deeply with one or more pigments of the carotinoid group, the resultant colour being red, orange, yellow or—rarely—greenish-yellow. Colourless droplets occur in many retinae either to the exclusion of coloured ones or in combination with them. Colourless droplets are usually small, which fact renders them prone to purely optical colourations under incompletely corrected lenses, and has led the majority of authors to describe various dilute green and blue droplets which actually contain no pigment and can exercise a selective filtration only if they fluoresce, thus slightly weakening one band of wave-lengths and slightly strengthening others.

The single large oil-droplet is invariably so located and of such diameter that no light-rays directed longitudinally to the cone can

reach the percipient organelle (the outer segment) without first passing through the oil-droplet. Some cones (e.g., the "red" cones of the domestic pigeon) have numerous tiny coloured droplets scattered throughout the inner segment in addition to the single large one, and in the accessory members of double cones a similar diffuse condition of the pigmented oil and the absence of a large droplet is the rule.

As we ascend the vertebrate scale, we find oil-droplets first in the sturgeons. Here they have been reported as yellowish (see Franz 1913, p. 33), but in the only sturgeon available to us (*Acipenser fulvescens*) they are colourless when observed through apochromatic lenses. The presence of only colourless oil-droplets in these, the most primitive forms which have droplets at all, has led to a belief that the oil droplet originated phylogenetically as a colourless structure whose sole function was to condense the incident light into an intense beam directed into the base of the photosensitive outer segment. We agree that it is plausible that the oil-droplet should have arisen as a colourless dioptric body, and that it should later, secondarily, have been "chosen" by the animal as a convenient *locus* for a pigmentation for which a need had arisen, but we do not believe that the situation in the sturgeon can be admitted as evidence. The sturgeon has a typical nocturnal eye; in *Acipenser fulvescens* there is a brilliantly silvery choroidal tapetum and the rods are large and greatly outnumber the cones. In this nocturnal form the oil-droplets would be expected to be colourless just as they are in the nocturnal lizard *Xantusia* (*v.i.*). In the latter case there can be no doubt that the oil-droplets have become colourless secondarily to facilitate the development of a nocturnal habit. Similarly in the case of *Acipenser* it is very probable that the absence of pigment in the oil-droplets goes with the animal's nocturnality and is secondary—that is, the diurnal ancestors of *Acipenser* may have had *coloured* oil-droplets.

Oil-droplets are definitely known to occur in at least one of the lung-fishes (*Lepidosiren;* Kerr, 1902, 1919). In immature retinae, Kerr found but one type of visual cell, and called it a rod—which, considering its form, was justifiable. If the visual cells of the adult *Lepidosiren* are actually physiological rods, their oil-droplets must be colourless. This, together with the temporary presence of an oil-droplet in the embryonic frog rod as reported first by Babuchin (1863, 1864) may signify that the oil-droplet once occurred in rods as well as in cones (if oil-droplets ever occurred in rods they were presumably colourless; there are, however, other interpretations of the above situations).

The frogs are the most primitive of living vertebrates which are known to have coloured oil-droplets. In these animals both yellow and colourless ones occur in roughly equal numbers. The

single pigment involved is the same carotinoid which colours the fat of the animal. Toads lack oil-droplets entirely, as do the salamanders and coecilians.

Of the reptiles, only the crocodilians, the geckoes and the snakes lack oil-droplets. The living Rhynchocephalian, *Sphenodon*, has long been known to possess them but observations of the fresh *Sphenodon* retina have not hitherto been made. At our request, Dr. W. P. Gowland of the University of Otago, Dunedin, New Zealand, kindly examined a fresh *Sphenodon* retina under apochromatic lenses and reported that definitely yellow droplets, like those of the domestic pigeon but larger, and having a greenish fluorescence, were present.

Sphenodon "sleeps the greater part of the day, and awakens slowly even when handled" (Hutton and Drummond, 1923), has a vertical pupil, and has relatively massive visual-cell outer segments. We had expected that *Sphenodon* would prove to have only colourless oil-droplets as do *Xantusia* and *Heloderma*; but *Sphenodon*, with its yellow droplets and shallow fovea, compares rather with the owls.

In the turtles many ruby-red, orange, yellow, and some colourless droplets are found. The lizards have (apochromatic optics!) only yellow and colourless ones; pigments are absent in *Xantusia* and *Heloderma* and absent or greatly reduced in fossorial forms such as *Aniella pulchra*. Like the Xantusiidae, the family Pygopodidae is characterized by a vertical-slit pupil and nocturnal habit; in these forms colourless oil-droplets are to be expected.

The birds have had the most attention. Many of the older workers employed microscopes which were not fully corrected for chromatic aberration, and in many cases illustrated their publications with vivid lithographs. The result has been that birds in general are erroneously credited by text writers with deep oil-droplet colours running the gamut of the visible spectrum. Few first-hand observations have been made by those persons who have been most interested in trying to fit the avian oil-droplet colours into the theories of colour-vision. Some authors have thus been led to think of the "blue" oil-droplets of birds as being as richly pigmented as the red droplets, whereas these droplets owe their faint bluish appearance solely to the optical properties of the pigment-free oil and to their critical diameters. Even pure green droplets are extremely rare; the majority of birds have some yellow droplets which are pure in colour and some which are greenish-yellow, but of the birds which we have examined, only one, the Flicker (*Colaptes auratus luteus*), has any droplets which are more green than yellow. The domestic pigeon, usually credited with eight distinct oil-droplet colours, shows only three under apochromatic lenses.

Of the mammals, the two lower divisions are claimed to have oil-droplets; the situation in the monotremes is, however, in considerable doubt. Gunn (1884) says, of *Ornithorhynchus*: "The bacillary layer is well-developed, consisting of both rods and cones. The outer segments of the cones are long and tapering. It was just possible to see oil-droplets at the outer ends of the cones in teased preparations. These were all of a light greenish colour . . ." Gunn's material had been preserved in *ca.* 50 per cent. alcohol (whiskey), and the structures he describes may have been merely shrinkage spaces, which often occur at the base of the outer segment. It is significant that these structures were omitted from the accompanying drawing, although the scale of the latter was such that even a small oil-droplet could have been shown. The objects Gunn saw must have been very small indeed, and were probably not oil-droplets.

Most marsupial mammals are nocturnal and lack oil-droplets. Droplets were found in two species of kangaroos (a diurnal group) by Hoffmann (1876), who stated the colours to be light blue, light green, and red. Unfortunately there has been no subsequent study of kangaroo material, and it is not known which of these droplets are actually pigmented. From analogy with the birds, we would suggest that the light blue droplets would be found colourless, the light green ones yellow, with apochromatic optics.

LENSES.

One of us has reported the discovery of *physiologically* yellow lenses in the eyes of diurnal snakes and diurnal squirrels (Walls, 1931). More recently the senior author has found yellow lenses in two lampreys *Entophenus appendix* and *Petromyzon marinus*. Lampreys are diurnal and most species have the same high proportion of cones to rods as is seen in the diurnal Sciuridae (unpublished observations). The pigment of the lenses of all three of these groups is apparently the same; it will be brought out later in this paper that this pigment is not identical with the true melanin which is often formed in early cataractous lenses, human and animal.

Physiological colouration of the living lens was first seen by Merker (1928) in the European squirrel, *Sciurus vulgaris*. Merker's discovery was of no interest to him, however; in fact, the colouration handicapped Merker in his work on the fluorescence of the lens, and he was concerned only in finding a solvent for it which would leave the squirrel lens colourless and in condition for his use.

Franz (1932) reports the presence of granules of pigment in some of the lens fibres in sections of formalin-fixed eyes of the European river lamprey, *Lampetra fluviatilis*; this pigment is

presumably the one which gives the lens its macroscopically homogeneous colouration. Franz refers to Plate (1924), who had found pigment granules in the preserved lens of the newly-transformed *Geotria chilensis*; neither of these authors noted the macroscopic colouration of the fresh lenses of lampreys.

CORNEAE.

The discovery of yellow lenses is, of course, too recent to have drawn the attention of the oil-droplet theorists. Yellow corneae, on the other hand, have long been known. Schiefferdecker (1887) found in the superior portion of the corneae of *Cyprinus carpio* and *Esox sp.* "a number of yellow pigment cells, which, inasmuch as they occur down to the middle of the pupil, probably influence colour-perception." No important function has ever been postulated for this corneal pigmentation, perhaps because its occurrence in many other fishes has not hitherto been noted[3].

We have found yellow corneae in a number of fishes; in some (*e.g., Esox vermiculatus, Amia calva*) the entire cornea is yellow —shading even to orange in the dorsal periphery. In other species there may be merely a yellow "eyeshade," the pigment not entirely covering the portion of the cornea through which the fish looks, so that the filter is apparently employed only when looking upward through the round window formed by the area of sub-total reflection in the water surface. This area is said to subtend a visual angle of about 97°. Thus it becomes difficult to decide, in many cases, whether or not the yellow colouration of the extreme dorsal region constitutes an effective colour screen. One gets the impression that the perfect yellow cornea, as in *Esox*, is merely a quantitative variant of a situation universal among fishes. One suspects that those fishes which have produced an effectively yellow cornea have done so independently, and more or less fortuitously. This opinion is strengthened by a comparison of *Esox* with, for example, *Cottus bairdii*. In the former the cell-bodies of numerous compact xanthophores are contiguous over much of the corneal surface; the entire xanthophore has migrated bodily and extensively from its original location in the pigmented head skin. In *Cottus*, on the other hand, the body of the cell has remained very close to the mass of pigment cells which enter into the head pattern above the eye, and has sent a very long heavily pigmented process down over the otherwise transparent cornea. The effect produced resembles a yellow waterfall, and gains the same end as the *Esox* arrangement.

3 Soemmering (1818) appears to have been the unwitting discoverer of the yellow cornea. Of *Esox* he says (p. 71): "I have observed the aqueous humour to be beautifully yellow, in the living fish under water, the golden colour being easily distinguishable because of the colourlessness of the cornea and lens."

We believe that the yellow cornea, unlike the yellow lens, has never been a group-character, but has been produced independently and variously in each genus which possesses it. Many swift, diurnal, sharp-sighted fishes—the trouts, for instance—lack the yellow cornea and all other types of filters; but these fishes might very well derive benefit from a yellow cornea if, like a minority of light-loving fishes, they had happened to hit upon it.

We should mention, in passing, another coloured cornea which probably has only an incidental relation to the present problem. We refer to the observation by Ditmars (1910; p. 140) of a *red* cornea in the *male* only of the Bahaman Iguana, *Cyclura bœalopha*. This observation has not been confirmed; without wishing to seem to doubt Dr. Ditmars, we would mention that in our survey of fishes for yellow corneae, we were often deceived by reflections from the iris which made the cornea appear pigmented when the line of sight was parallel and close to the side of the head; only when the cornea was excised, and placed over a white background, could we be certain that the colour was actually there. The cornea of *C. bœalopha* may similarly owe its appearance to reflection, and the question of its colouration must remain open until the excised tissue is examined. In any case the meaning of such a colouration remains a mystery to us; as will appear later, a red cornea would be explicable in terms of our own conclusions if it were present in both sexes and if *C. bœalopha* were aquatic. Ditmars, however, states that this species, unlike some others of the genus, is terrestrial. It may be found that the oil-droplets of the male are paler than those of the female or even colourless, but this would be more of an effect than a cause of the male's red cornea[4].

Retinal Capillaries and Maculae Luteae.

A retinal capillary network is characteristic of the mammals; of lower forms, only the eels have vascular retinae. Indeed, many of the mammals (see Leber, 1903) lack retinal capillaries. Schultze (1873)[5] long ago pointed out that the human retinal capillaries form an effective filter and absorb much violet and some blue. The reader may be inclined to doubt this, for the capillary supply naturally appears scanty and haphazard in a thin section; but it

4 Cilimbaris (1910) describes a homogeneous pigmentation of the entire surface of the cornea in the sheep; the chromatophores were observed in sections, in all individuals studied. No observation was made of the fresh cornea, which may have been yellowish macroscopically.

The breed of sheep was not mentioned, and the phenomenon is apparently restricted to certain breeds and probably fortuitous—at least, we failed to find chromatophores or free pigment in the fresh cornea of a Rambouillet ewe (*ca.* 1½ years old). Although no pigment was seen, this cornea was distinctly cloudy—but not coloured.

5 For convenience we shall refer throughout to this inclusive publication, rather than to Schultze's separate papers of the preceding decade.

should be remembered that in a flat view of the retina there are but few small areas of the bacillary layer which are not covered by capillaries at some level. Moreover, the capillary network is considerably out of focus, and there is, therefore, less need for it to be free of projected lacunae in order for it to constitute a filter; as a filter it is, of course, yellow, not red, because of the thinness of the blood streams.

Deep and well-developed foveae occur in many of the lower animals. The only mammals which have such a fovea are the diurnal primates (Woollard, 1927; Kolmer, 1930); and it is in just these forms that the yellow pigmentation of the foveal region, the "macula lutea," is seen. The macular pigmentation is another familiar but unsung intra-ocular colour-filter. Several ophthalmologists have pointed out that it necessarily reduces the apparent intensity of a blue or violet stimulus, but there has not been much attempt to account for it in terms of a positive value in vision (see, however, Holm, 1922). Foveae in the lower animals, if well-developed, contain oil-droplets (shallow foveae such as those of the pipe-fishes and sea-horses have no oil-droplets, but the eyes of these forms may have yellow corneae—they have not yet been examined). It would seem that the macular pigment of the primates replaces the yellow oil-droplets of the birds and lizards and the yellow lens of the few snakes which have good foveae (*Dryophis* and probably *Dryophiops* and *Thelotornis*—see Walls, 1932*a*). At the same time, as Lindsay Johnson has pointed out, the macular pigment replaces the capillaries, which are lacking only in the foveal region because of the thinning which takes place there.

The macular pigment of the diurnal primate is thus a stop-gap, filling in the one avascular portion of the retina and constituting a more effective filter than would the capillaries, even were the latter present in the fovea; this is indicated by the fact that a blue or violet light appears brighter peripherally than when fixated centrally[6].

The accompanying Table I summarizes the entire situation. It will be seen that there is every indication that, *whatever* the significance of a yellow filter, such filters are needed only by *diurnal* forms. A highly absorptive yellow filter is actually a handicap to nocturnal forms, for only brute vision, at best, is possible for any eye in dim illumination, and a yellow filter would not only

6 The presence of numbers of rods at and near the edge of the macula may be a potent factor in this phenomenon. Rods have been held by many investigators to be capable of qualitative hue-perception at the short end of the visible spectrum; see Siven (1905, 1912), Friedman (1931), and especially p. 66 of the review by Adams (1929).

TABLE I

DISTRIBUTION OF INTRA-OCULAR COLOUR-FILTERS IN VERTEBRATES

GROUP		HABITS WITH REGARD TO LIGHT	RETINAL OIL-DROPLETS	YELLOW LENS	YELLOW CORNEA	RETINAL CAPILLARIES	MACULA LUTEA
CYCLOSTOMES	Lampreys:	DIURNAL		+			
	Hags:	Blind					
ELASMOBRANCHS	*e.g. Isurus:*	"DIURNAL"					
	Nearly all:	Nocturnal					
GANOIDS	*e.g. Amia:*	DIURNAL			+		
	e.g. Acipenser:	Nocturnal	+ All colourless				
DIPNOANS	*e.g. Lepidosiren:*	Nocturnal	+ All colourless				
TELEOSTS	Many (*e.g. Esox*):	DIURNAL			+In some		
	Many (*e.g. Percopsis*):	Nocturnal				+ In eels only	
AMPHIBIANS	Coecilians:	Fossorial					
	Salamanders:	Secretive					
	Salientia — Frogs:	DIURNAL	+ Yellow				
	Salientia — Toads, Hylas:	Nocturnal					
REPTILES	Turtles:	DIURNAL	+ Red, Orange, Yellow				
	Crocodilians:	Nocturnal					
	Sphenodon:	Nocturnal	+ Yellow				
	Lizards — Most:	DIURNAL	+ Yellow		*		
	Lizards — Anniellidae, etc.:	Fossorial	+ Almost colourless				
	Lizards — Xantusiidae, Helodermatidae:	Nocturnal	+ All colourless				
	Lizards — Geckoes (most):	Nocturnal					
	Snakes — Many:	DIURNAL		+			
	Snakes — Many:	Secretive, Nocturnal					
BIRDS	Most:	DIURNAL	+ Red, Orange, Yellow				
	Some:	Nocturnal	+ Mostly colourless				
MAMMALS	Monotremes:	Crepuscular, Nocturnal	Colourless?				
	Marsupials — Some Macropodidae:	DIURNAL	+ Colours?				
	Marsupials — Most:	Nocturnal				+In some	
	Placentals — Most:	Crepuscular, Nocturnal				+In some	
	Placentals — *Ochotona:*	DIURNAL				?	
	Placentals — Sciuridae — Most:	DIURNAL		+		+	
	Placentals — Sciuridae — Pteromyinae:	Nocturnal				+	
	Placentals — Primates — Many:	DIURNAL				+	+
	Placentals — Primates — Many:	Nocturnal				+	

* *Red* cornea, in *male* only, in *Cyclura bœalopha*.

TABLE I—*continued*

THE FOLLOWING FORMS SHOULD BE EXAMINED:

Crossopterygians: *(Polypterus, Calamoichthys)*	?	?	?	?	
Lepidosiren; Polyodon; Pygopodidae; Monotremes:		Colourless?			
Phelsuma, Lygodactylus; Procavia; Tupaia:			?	?	
Kangaroos:		Colours?			
Pikas *(Ochotona)*:					?

be a useless refinement but would further reduce the illumination which is perhaps already barely liminal.

The yellow or orange oil-droplet is only one form of yellow intra-ocular colour-filter, and other types appear only where oil-droplets are lacking.

As during vertebrate differentiation the habit of diurnality has evolved and disappeared and arisen anew, yellow filters have come and gone also. There is no definite succession of types; the vertebrate series presents no picture which would indicate that the various types of yellow filters were each evolved to replace an inferior mechanism. The yellow lens, the yellow cornea, and the complex of capillaries and pigment typical of the human retina are all on a par. The oil-droplet mosaic, however, has at least one obvious point of superiority: the lizard, for example, with both yellow and colourless droplets, can receive the advantages of the yellow filter and at the same time perceive (with those cones which contain no pigment) weak, short-wave stimuli. The lizard, if it has colour-perception, can thus discriminate hues over as wide a band of wave-lengths as can man; at the same time, the lizard gains the same advantages, whatever they may be, that are conferred by a yellow lens or macular pigmentation. The squirrel, on the other hand, sacrifices perception in the short end of the spectrum by placing a homogeneous filter in front of all visual cells alike. To express the table in story form:

The yellow lens is apparently the most primitive type of colour-filter; it makes its début in the lampreys, where the pigment involved seems to be identical with that in the lenses of the snakes and squirrels. This peculiar distribution indicates that the precursors of the pigment are easily available and that the pigment is readily produced on, so to speak, short notice.

Very few of the elasmobranch fishes could possibly be considered diurnal; one of these, the Bonito Shark (*Isurus glaucus*)

along with several nocturnal species (*Rhinotriacis heulei, Mustelus californicus, Triakis semifasciata,* and *Alopias vulpes*) was kindly examined for us by Miss Frances N. Clark, of the California State Fisheries Laboratory. No yellow colouration of any of the media was found.

The "diurnal" elasmobranchs are thus our first exception to the rule of yellow filters being associated with diurnality. There is considerable experimental and anatomical basis for the widely-held belief that the eyes of elasmobranchs mean little to them; if this may be assumed to be true for the Bonito Shark, it may account for the absence of such a refinement as a yellow filter.

In the Ganoids and their relatives, the known bright-light forms (*e.g., Amia*) have well-developed yellow corneae. The nocturnal *Acipenser* has colourless oil-droplets, indicating that in diurnal ancestors these were probably coloured; if we assume this it would appear that the diurnal ancestors of the sturgeon lacked a yellow cornea. *Lepidosiren* probably has colourless oil-droplets, and the mud-loving *Polyodon*, closest living relative of the sturgeons, probably has colourless oil-droplets if any; so also with the lungfish *Neoceratodus*, which Dean (1906) states to be nocturnal, and *Protopterus* which is apparently also a night-prowler.

The Teleosts appear, like *Amia*, to have evolved from primitive ganoids, which had not yet produced the oil-droplet. A minority of light-loving Teleosts have yellow corneae. As we have already stated, we consider the yellow cornea to have arisen independently many times, and believe that a fish which lacks it has not necessarily "tried" it and found it undesirable.

Unless the oil-droplet of the frogs is a re-invention, the primitive amphibians were probably diurnal; else the oil-droplet inherited from the Ganoids would surely have had time to vanish completely as it has in the snakes, placental mammals, etc. The droplets have been lost in the Bufonidae and Hylidae, and are likewise lacking in the salamanders and coecilians.

Again, unless the turtle's oil-droplets are innovations, the dominant reptiles of the past were diurnal. The crocodiles being nocturnal forms of long standing have discarded the oil-droplets entirely. The turtles, a very ancient group, have retained and diversified them; here, for the first time, there is more than a single colour in the same retina. A second advantage of the oil-droplet type of filter over all other types is seen in this very diversification, for only if the individual visual cell has its own private filter is it possible for the filter to differentiate and serve more than a limited function. We shall present later our evidence for considering that the red oil-droplet is concerned primarily with a rather different process from the yellow-orange one.

Lizards have no pure colour other than yellow. The geckoes, an almost bodily nocturnal group which early diverged from the lacertilian stem, have lost the oil-droplets, although their visual cells are descended from lacertilian cones[7]. One or two genera of geckoes (*e.g., Phelsuma, Lygodactylus*) are markedly diurnal; these forms should be investigated for yellow filters of some type or other.

In many modern families of lizards, forms with partially or wholly reduced limbs occur. From ancient equivalents of such forms the snakes unquestionably originated. An interesting side-light on the early history of the snake is, we believe, afforded by the intra-ocular colour-filter situation. The snakes lack oil-droplets, but the swift, active diurnal forms have considerable lens pigment, the secretive forms practically none, and the nocturnal species none whatever (see Walls, 1931). The "original" snake must have had such a mode of life that it could afford to discard the oil-droplets of its lizard ancestors; the first snakes were, then, secretive or nocturnal, and must have remained so for a considerable time—for so archaic a lizard as *Xantusia* has lost the colour of the oil-droplet, but has retained the droplet itself. The snake group subsequently differentiated and produced a central family, the Colubridae, which contains a majority of diurnal species. These diurnal forms, coming in need of a yellow filter, re-invented the yellow lens. This situation in the snakes leads us to conclude that once the oil-droplet, which is a definitely structural entity, is lost it cannot be reproduced by a descendant group. The yellow lens on the other hand, representing merely a minor chemical modification of a standard structure, has reappeared at least twice in vertebrate evolution.

The oil-droplets of the birds were passed on to them by their diurnal reptilian ancestors; it cannot be decided whether the red droplets of birds were produced by them or have common ancestry with the red droplets of the turtles. We incline, however, to the former view; our reason will not be apparent until later in this paper.

The early mammals possessed oil-droplets; their presence in the living monotremes is doubtful as pointed out above. The nocturnal and crepuscular habits of these forms as reported by Bennett (1860, p. 136; p. 149) and Burrell (1927) lead one to suspect that their oil-droplets, if any, are colourless.

Of the marsupials, only the diurnal forms (the kangaroos) have kept the oil-droplets; these forms have no retinal capillary circulation. The placental mammals, typically, do have retinal

7 The visual cells of the nocturnal geckoes are universally regarded as rods. They are indeed functionally such; the evidence for the view expressed above will be presented by the senior author in a future paper.

capillaries; but that the vascularization of the retina of the placental mammals did not in itself make unnecessary an oil-droplet filter is indicated not only by the fact that retinal capillaries are present in some marsupials, but also by the fact that, like these marsupials, most placental mammals are nocturnal or crepuscular and have retinal capillaries. If the capillaries are so ineffective a filter that they are tolerated by nocturnal forms, they cannot be considered the equivalent of a deeply pigmented oil-droplet system.

It is probably not fully realized by a majority of biologists that the placental mammals, as a group, are crepuscular or nocturnal. Many forms have the habit of taking "cat-naps" in the day time with intervening periods of, apparently, full activity; but many such species employ the protecting darkness in migrations of any great extent. Domesticated mammals readily invert their habits to accommodate to those of their masters, but "escapes" revert to an inherent crepuscularity or nocturnality. The hunted mammal usually awakens to full activity and gets into motion before the approaching hunter sees his quarry at all. All of these factors help to blind one to the truth of the above generalization.

Few of the placentals are strictly diurnal; those available in this country are the diurnal members of the Sciuridae. The tree-squirrels (excepting the nocturnal flying squirrels), the chipmunks, ground-squirrels, and marmots all have yellow lenses, the intensity of the colouration correlating nicely with the extent to which the species exposes itself to bright light (see Walls, 1931). With the exception of the squirrel family, a single diurnal genus of placental mammals occurs in the United States. These forms are the Pikas, which are active in daylight hours except for a period centering at noon when their rock-slide habitats are unbearably hot. The Pikas may have a rich retinal capillary network, but they have no other type of intra-ocular colour-filter; Dr. Carl Russell, of the National Park Service, kindly examined the media of three specimens of *Ochotona princeps ventorum* at our request, and reported the lens and cornea perfectly colourless.

Besides the above, some of the primates, some of the insectivores (*e.g.*, *Tupaia*), and the Hyrax (*Procavia*) are stated in the natural history literature to be diurnal. *Procavia* has little or no retinal circulation (Leber, 1903) and demands examination for filters of other types. The eye of *Tupaia* has never been investigated from this standpoint.

In the diurnal primates, man for example, the need for a yellow filter is apparently not so great as in the even more strictly diurnal Sciuridae which, according to incomplete investigations of the senior author, are exceptional among mammals in having at least as many cones as rods (see also Grosskopf, 1893). In any event

the diurnal primates are adequately served by the combination of retinal capillaries and macular pigmentation.

The reader will of course have noted that we have said nothing as to variations in the richness of the retinal capillary circulation from species to species. Unfortunately, we have no data on this point. For the sake of our thesis, we would naturally be pleased to learn that *Ochotona* has a thick retina heavily laden with capillaries and that the extremely nocturnal *Didelphys* has but few, as is indeed known to be the case in the bats. We can only suggest that the study of injected total retinae of some of these exceptional forms might be worth while.

We must emphasize that we do not at all consider that the important functions of nutrition and respiration are subsidiary in any way to the secondary and actually fortuitous filtering capacity of the capillaries. Forms which *seem* to need a yellow filter, *e.g.*, *Ochotona*, cannot be expected to abuse the metabolism of their retinae to obtain one by over-development of the capillary network; nor of course can nocturnal forms afford to discard the capillaries in order to eliminate a slight handicap. It should also be remembered that in afoveate mammals the area centralis when present is generally avoided by blood-vessels (Franz, 1913).

Possible Interpretations

It having now been demonstrated that diurnal vertebrates in general have intra-ocular filters of one type or another, and that nocturnal forms have not produced such filters, have discarded those effective types which diurnal ancestors handed on to them[8], and will tolerate only the weakest of all types (the capillary network), we must now attempt an explanation of this situation. Two questions are involved: Why is a *yellow* spectacle desirable for *all* diurnal vertebrates? Why do the turtles and birds (and kangaroos?), with so little in common in their environments and adaptations, hold a joint monopoly of an additional *red* filter? Since the various theories have been concerned almost solely with the best-known type of filter, the oil-droplet mosaic, we will consider this type first.

The various theories either attempt a single explanation of all of the avian oil-droplet colours, or account reasonably for but one of the colours; in the latter case the presence of more than one colour is left unexplained. While our chart brings out the widespread occurrence of *yellow* filters other than those constituted by the oil-droplets, it should be remembered that this synthesis is

[8] *Sphenodon*, combining yellow droplets with nocturnality and a vertical pupil, is an exception here.

new; we shall see that where attention has been given chiefly to one oil-droplet colour, it is the *red* rather than the yellow which has had most consideration.

The oldest theory of all is the one which is still most frequently seen in text-books; this is the "colour-vision theory" of Krause (1863). This author based his theory at first upon a misconception as to the number of distinct colours present in lizards. Later, Krause (supported by Max Schultze) shifted the basis to the birds, for the more complex situation in that group seemed to serve much better the purpose of the theory. The colour-vision theory then is based at the present time on the colour assortment of the diurnal avian droplet mosaic, a tacit implication being that vertebrate groups with fewer droplet colours must have a correspondingly reduced hue-discriminatory capacity. The present form of the colour-vision theory may be stated as follows:

Unlike the droplet-free placental mammal, the bird has but a single undifferentiated photochemical substance in its cone outer segments. This substance is broken down by any or all visible wave-lengths and initiates an impulse. If rays of all wave-lengths had access to every cone, achromatic vision would result, for the single photochemical substance cannot "discriminate" qualitatively between wave-lengths. The coloured oil-droplet of a given cone permits only certain wave-lengths to affect the outer segment of that cone; thus some wave-lengths are permitted to stimulate only certain cones and other wave-lengths affect only certain other cones. A basis is thus laid for hue-discrimination, the hues perceptible centrally as qualitative entities being determined by the transmission bands of the various oil-droplet types.

Krause, who was never convinced of the non-existence of blue-pigmented oil-droplets, saw in the avian colour assortment the specific filters for the "Urfarben" or primary colours, demanded by the Young-Helmholtz theory of colour vision (see Krause, 1894). Comparisons of the droplet mosaic with the tri-colour granulation of a Lumière plate and with the three-colour process of reproduction have often been made; the discussions in Frisch (1904) and Garten (1907) are perhaps the most elaborate.

Consideration of this plausible theory leads to certain doubts. There can be no question that Teleosts have colour vision (see Warner, 1931), yet they have no oil-droplets. It is puzzling that an oil-droplet mechanism for colour vision should begin to evolve in the Amphibia, with yellow as the only hue discriminable, and become perfect (except as to the perception of short-wave hues) only in the taxonomically and chronologically distant birds—when the lowly Teleosts had been able to produce a more perfect mechanism based upon a differentiated photochemical system, a mechanism which would reappear only in the placental mammals.

Again, it is curious that the placental mammals should have so quickly revolutionized the colour vision mechanism, for the so closely related marsupials (kangaroos) have been unable to abandon the oil-droplets. If we assume that all vertebrates which discriminate hues, as such, do so by the teleostean and human method, the oil-droplets become seen as *modifiers* of colour-vision for which a necessity may still be found.

These are not, however, grave objections to the colour-vision theory; the fatal blow is given by the birds themselves.

Schultze (1873) says: "According to my observations the percipient elements in the two fossae centrales of the falcon[9] consist of cones of smaller thickness than in the adjoining parts, which possess only yellow, but no red pigment spheroids, though both are present in the other portions of the retina." Krause (1894) records an identical situation in a hawk, *Buteo vulgaris*, and cites Schultze as having found a preponderance of yellow droplets in the foveae of *Corvus corone* and *C. cornix*, so that the pattern is "like the edge of the fovea of *Buteo vulgaris*."

These observations have gone unnoticed; the authors themselves do not appear to have realized their significance and no other oil-droplet theorist has taken them into consideration. The assumption by all that the colour pattern in the avian fovea is the same as in the general fundus is due, we think, to the fact that the mass of research upon oil-droplets has been made on the domestic fowl and the domestic pigeon. The former has no fovea and the latter a degenerate one from which the red droplets are not excluded. Waelchli (1881, 1883), whose work on the pigeon is regarded as classical, makes no mention of an alteration of the colour proportions in the fovea comparable with the situation in the birds mentioned above. In the afoveate fowl the area of most acute vision (the "orange field"—see Krause, 1894) is evenly dotted with red, orange, and yellow droplets[10].

The explanation of these diverse situations is easily seen in the relative importance of the fovea in different birds. As Krause and others have pointed out, the absence of a fovea in the fowl (and its barn-yard associates) is correlated with its complete domestication; the pigeon, less perfectly domesticated, is well known to have a shallow and variable fovea (see Slonaker, 1897). One would expect to find a well-developed fovea in the crows and ravens and an even more perfect development in the diurnal predators—most especially in the swift-stooping falcons.

It appears then that the perfect avian fovea contains only yellow

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[9] *Falco s. subbuteo?* We have confirmed these observations on a specimen of *Falco sparverius.*

[10] The turtles are also afoveate, hence do not reveal the physiological divorce of the oil-droplet colours.

droplets and that red droplets invade this critical region only when, as in the pigeon, the organization of the fovea begins to break down[11]. The final loss of the fovea, as in the fowl, involves a concomitant obliteration of the exclusively yellow portion of the droplet mosaic.

To return to the colour-vision theory—it is now seen to be inconceivable that a bird should have polychromatic vision in the relatively subsidiary periphery and only monochromatic vision in the all-important fovea. The picture can have but one meaning, a meaning which is pointed to also by the comparative situation not only in the groups which have the yellow droplet alone, but also in those which have some altogether different type of yellow filter: *the yellow droplet is the more important for the bird's vision; the red droplet is primarily concerned in some process distinct from and secondary to the function of the yellow.* The avian colour-filter situation is indeed complex—but not in the direction assumed in the colour-vision theory.

The older literature of the colour vision of the fowl has been interpreted as supporting the colour-vision theory of oil-droplet function. The absence of blue-pigmented droplets being now universally admitted, the supposed blue-blindness of the hen has seemed to many a very strong indication that the ability of the bird to discriminate the longer-waved hues is due to the selective filtration of the red, orange, and yellow oil-droplets. The argument is, of course, that the hen cannot discriminate blue as such, because she has no blue oil-droplets (see Garten, 1907).

The question of the fowl's blue-blindness is highly controversial. The work of Hess (see 1912) seemingly established the fact beyond doubt. The principal technique employed consisted of projecting a spectrum upon a floor, sprinkling rice grains uniformly throughout the (to the human) visible region and allowing a light- or dark-adapted hen to feed upon the grains. The fowls were observed to eat the grains throughout the (human) long-wave region, but they ceased to peck in the neighbourhood of the blue-green junction. The conclusion drawn was that the blue and violet regions were as darkness to the bird, the explanation being that the short rays were absorbed by the oil-droplets.

The presence of many colourless droplets and of cones (the accessory members of the double cones) which contain no oil-droplets would lead us to expect that while perhaps (in terms of the theory) the hen may have no "blue" or "violet" sensations, still such rays should stimulate the cones of these two categories. Objects in the short-wave end of the spectrum should thus be visible, though not (due to the coarseness of the colourless-cone

11 There are some bright-light birds in which very few red droplets are present anywhere in the retina (*e.g.*, barn swallows, martins; see Krause, 1894).

mosaic) sharply outlined and perhaps not chromatic. One would expect that *large* objects in the blue and violet would surely be perceived and this was indeed found to be the case by Blässer (1926)[12].

If the light-adapted hen sees the rice grains in the blue and violet one wonders why she does not eat them. If they appear achromatic to her, her failure to consume them is wholly mysterious; but if they appear coloured to her, the logical explanation (given by Hahn, 1916) is that blue objects do not look good to eat, there being no blue food in nature so far as the hen is concerned.

Hahn (1916), using the feeding-in-a-spectrum technique, concluded that while the hen has an instinctive "blue-shyness" she can be trained to overcome it and then no longer appears to have a relative blue-blindness. Hahn believed that the colour vision of the fowl is much like that of the normal human, but Blässer (1926) criticized her technique, the intensity of Hahn's arc-light illumination having been variable and high so that reflection from other grains may have illuminated those in the short-wave region.

Honigmann (1921) made the interesting discovery that the light-adapted fowl is much more sensitive to the longer wave-lengths than is the light-adapted human. He found that the relative blue-blindness increases markedly after sexual maturity, presumably due to an increase in the size (and pigment content?) of the coloured oil-droplets.

Blässer (1926) confirmed the existence of a *partial* relative blue-blindness in the fowl and believed that the bird would see all colours brighter than man were it not for the absorption of much of the short-wave light by the oil-droplets.

None of the above authors appears to have known of the work of Watson (1915) and Lashley (1916), who by a vastly superior method involving the training of the birds to saturated spectral lights, proved beyond cavil that the fowl perceives hues as such and has a spectrum almost identically co-extensive with that of man.

Owing to an unfortunate lacuna in Lashley's work it cannot be regarded as absolutely proven that the fowl sees blue and violet as qualities distinct from each other, and from green, etc., but it is certain that some of her cones are stimulable by short-wave lengths. While we believe that the exclusion of red droplets from the avian fovea is an insurmountable obstacle to the success of the colour-vision theory, we await with interest an eventual continuation by some investigator of Lashley's experiments into the blue-violet region. We feel safe in drawing the conclusion that the

[12] Who however credits the rods with this perception. There are few (or no) rods in the portion of the fowl's retina used in pecking, but Blässer was forced to his conclusion because he could find no droplet-free cones and no colourless droplets.

light-adapted hen perceives blue qualitatively[13], else she would eat grains unquestionably visible to her in the short-wave end of the spectrum. Further confirmation will remove the last prop of the colour-vision theory, for if the hen secures the sensations of blue and violet without blue oil-droplets, her droplets cannot *endow* her with colour-vision but merely *modify* the values of hues which are discriminated by an altogether different mechanism, presumably a differentiated photochemical system.

The second theory of oil-droplet function to be offered was that of Hensen (1865), revived later in modified forms by Waelchli and Hess. Hensen thought that the oil-droplets serve colour vision by adjusting the chemical effects of the various wave-lengths; by absorbing relatively larger proportions of the more powerfully actinic short wave-lengths, the droplets equalize the capacities of the respective rays for producing the chemical changes which initiate the visual impulses.

The supposed advantage of this operation would be that the spectrum would be rendered homogeneous in physiological brightness (subjective intensity), and thus the various hues of the visual field would have equal voice in the sensation complex of the percipient. The first doubt which arises derives from the fact that man certainly has no special mechanism (extra-macularly, at least) which would materially alter the relative actinic power of different lights. The spectrum, even when subtended only by the pigmented macula, is notoriously non-uniform in physiological brightness both to the light- and dark-adapted eye; but man does not appear to be thereby handicapped.

Waelchli (1883) held an opinion similar to Hensen's, but seems to have had the "harmful" effects of short-wave light more definitely in mind. He saw in the macular pigmentation of the primates a similar protective mechanism. Waelchli's ideas foreshadowed those more definitely expressed by Hess.

Hess believed for several years that the function of the coloured droplet was the elimination of those actinic rays known to be lethal to protoplasm. The clear portions of the eye are exposed to light, including ultra-violet light, as are no other unpigmented living tissues. Hess thought that the oil-droplet[14] protected the sensitive outer segment from harmful ultra-violet irradiation. Hess himself became dubious of this explanation when he found himself forced to assume that the cones of turtles would be greatly

[13] And see the excellent paper of Bailey and Riley (1931); these authors concluded that the parakeet *Melopsittacus undulatus* has essentially the same hue-discriminatory capacity as man, and found that this bird discriminates blue, green, etc., on a qualitative basis.

[14] And the macular pigment of primates; but no abiotic ultra-violet light reaches the human retina (Duke-Elder, 1929).

harmed even by visible wave-lengths (because even "nocturnal"[15] turtles have richly coloured oil-droplets). He admitted also that in terms of this theory the lizards, exposed to bright sunlight, should have much more deeply pigmented oil-droplets than they possess. Hess pointed out that the reduction or absence of the colours in nocturnal birds is correlated with their lessened exposure to ultra-violet light; but any other supposed need for colour-filters finds this same support (we maintain that no matter what the function of intra-ocular filters may be, their absence or great reduction in nocturnal species is to be expected).

An obvious objection applies here and also to Hensen's theory: not more than a single type of droplet would be needed, and *all* cones should contain such a droplet. An ideal pigmentation (red?) should have been evolved long ago and rigidly adhered to, if the reduction of the chemical effects of certain wave-lengths or the protection of the percipient organelle from abiotic light were its function.

Erhard (1924) thinks that while oil-droplet and macular pigments may be protective in this manner, the same protection could have been afforded by a capacity for fluorescence of one or more of the colourless dioptric media. He seems to think that the birds should have evolved such a fluorescence, as have other vertebrates and some insects (Hess, 1911*a*; and see Stübel, 1911, Merker, 1928), instead of resorting to the absorption-by-pigment method with the detrimental effect thereof on colour values.

The fundamental question here is whether any ultra-violet light within or near the abiotic range (λ2950-3050; Verhoeff and Bell 1916) ever actually reaches the vertebrate retina. The human optic media transmit absolutely no ultra-violet below λ3200 (Duke-Elder, 1929); hence the human retina is shielded from these harmful rays by the unpigmented cornea and lens. In other vertebrates these tissues *might* be transparent to abiotic rays, or the absorption might not be complete in the short distances involved in very small eyes, thus necessitating a more efficacious absorbent in the form of a pigmented filter—which should, logically, be yellow, orange, or red.

To ascertain whether abiotic light reaches the retina in a droplet-bearing eye we performed a simple experiment:

The domestic pigeon was chosen, as a species in which the oil-droplet mosaic is well developed. An eye was removed from a

[15] Few of the many turtles termed "nocturnal" by Hess (1910) are such to any degree whatever. All are active in daylight, feeding and basking; the Kinosternidae and Chelydridae are, however, more active at night than other families. Nocturnal activity does not imply scotopic vision, especially in the case of aquatic animals whose chemical senses are very keen.

Henning (1920) sees no ophthalmological foundation for scotopic visual capacity in any of the turtles, but one of us (G.L.W.) has found rods in the retina of *Chelydra serpentina*.

freshly killed adult bird; with a Gillette blade, a cut was made posterior to the equator of the globe and parallel to the plane of the iris. Much of the posterior wall and the greater part of the retina were thus removed while the major portion of the vitreous, uncontaminated by blood, retinal fragments, or the like, remained in place in the globe. The large anterior moiety of the globe was now wrung on to a thin (1.5 mm.) quartz disc, which retained the vitreous and permitted the optic axis to be placed horizontally.

The eye was now placed in the beam from a 12 mm. tungsten spark (under water); this beam, very rich in ultra-violet, passed through the cornea, aqueous, pupil, about one-half of the original thickness of the vitreous, and the quartz plate into a Hilger quartz spectrograph.

Exposures were made with proper plates at thirty seconds and at one minute; even with the latter exposure there was no transmission whatever below λ3120 and very little between λ3120 and λ3150. Since no harmful actinic light can reach the pigeon's retina, it is obvious that none of the coloured oil-droplets can possibly be designed to absorb such light. Nor, of course, can such absorption be a function of the primate macular pigment! It is possible that in very small eyes (*e.g.*, those of brook lampreys) the pigment of the lens may share to a valuable extent in the protection of the retina, but there are many small diurnal fishes with small eyes, which do nicely without such a pigment[16].

The theory of Haab (1879) is least reasonable of all. Haab was struck by the tendency toward mutual exclusiveness of well developed oil-droplet patterns and visual purple. Vertebrates which have much visual purple have few oil-droplets, and *vice versa* (but this is merely a reflection of the duplicity theory). The untenability of Haab's conclusion—that the oil-droplet pigments have the same function as visual purple—has been explained by Garten (1907) and others. The oil-droplet colours are remarkably light-stable, which Haab himself knew (see Kühne and Ayers, 1878) and cannot be considered photochemical substances comparable with visual purple or with the hypothetical ones required by the multi-component theories of colour vision[17]. Moreover, as Garten points out, the oil-droplet is in a disadvantageous position in the cell for it to be the locus of a photochemical activity involved in the visual act.

[16] It is worthy of note that most of the filterless diurnal vertebrates are fishes. Aquatic forms probably receive considerable protection from ultra-violet light through the high capacity of natural waters for fluorescing such light (see Merker, 1931). It should be remembered that the vertebrate lens is more fluorescent than any other part of the body (Stübel, 1911; Merker, 1928).

[17] Hamada (1927) has, however, demonstrated a photochemical difference between the oil-droplets of dark- and light-adapted frog cones, expressed in a staining difference with toluidin blue-erythrosin.

The above theories view the oil-droplets as neutralizers of physiological defects or as substitutes for other mechanisms; we turn now to a new set of ideas concerned with the possible values of the oil-droplets as optical devices for the positive improvement of vision beyond the level attainable without them.

Hess believed the droplet to act as a spherical lens, concentrating the longer wave-lengths into an intense pencil directed into the outer segment, thus putting to work the light which would otherwise escape past the sides of the relatively slender outer segment and "go to waste" by being absorbed in the pigment epithelium. This theory takes no account of the pigments or of their differentiation, but may explain the retention of completely decolourized droplets by such forms as *Heloderma* and *Xantusia*.

Honigmann (1921) considered this concentration a probable factor in the supersensitivity (compared with the human) of the retina of the fowl. Erhard (1924) calls attention to the slenderness of the outer segment as a factor in visual acuity, and points out that a corollary of increased slenderness is a reduction of the amount of light entrapped by the cross-sectional area of the outer segment; the concentrating action of the oil-droplet would counterbalance this[18].

Garten (1907), while he supported the colour-vision theory, proposed an extra function for the red oil-droplet—the reduction of chromatic aberration; the shorter wave-lengths, being the more refrangible, are responsible for the greater portion of the "thickening"[19] of the image, and their removal would naturally result in a thinner image, the elimination of blur circles, and a consequent increase in visual acuity. It is well known that in lithographic establishments, etc., attempts are made to furnish light as nearly

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18 We feel that too much attention has been paid in the past to the diameter of the outer segment as a factor in the structural basis for the two-point limen. The diameter of the inner segment is the important value; in such cones as those of man the gentle curvature of the outer end of the inner segment and of the fibrils of the "Fadenapparat" is such as to guide light rays into the outer segment without permitting lateral escape. When this is borne in mind, resort to the extreme theory of Fortin or even to the less unreasonable one of Bard (1919) becomes unnecessary.

The ellipsoid, a single solid body in most cones but represented in human cones by the "Fadenapparat," has the same action which Hess ascribes to the oil-droplet. If the condensing action of the oil-droplet is important, one wonders why the ellipsoid is invariably present even in cones which contain oil-droplets.

We have already mentioned our lack of sympathy with the view that the absence of pigment in the sturgeon's droplets indicates that the droplet was originally an achromatic body with a purely dioptric function. The pigment epithelial cells of many animals contain droplets of yellow oil; these may be genetically related to those of the visual cells, which may thus have been pigmented from the beginning. In the frogs, the lowest forms which have pigmented droplets, the pigment and oil of the droplets in the pigment cells and in the cones are identical (Majima, 1925), and the same pigment colours the somatic fat (Palmer, 1922).

19 The "thickness" of the image, in our sense, being equal to the linear chromatic aberration.

as possible *monochromatic*; for monochromatic light of *any* wavelength should theoretically result in maximal visual acuity (in small visual fields) if its intensity is of the correct value. Only monochromatic light can eliminate *all* chromatic aberration. Garten also speaks of the coloured droplets as eliminating, from the mosaic image, the scattered short-wave light which succeeds in reaching the eye through mist-filled distances.

Henning (1920) has elaborated upon Garten's views and adduced many points to their support. He had previously (1919) called attention to the effect of red light in increasing visual acuity and apparent size.

Henning claims that both photography and human vision are much improved in misty weather by the use of red, orange, or yellow filters, and that the same improvement is obtained in vision through water which is in the slightest degree unclear; the longer waves penetrate best through turbid and watery media of all kinds. He states that the red and yellow lights of an approaching steamer are seen first through a mist, and that persons with turbid optic media find that they can read more clearly if they use red light. The same effect is produced whether one looks at objects illuminated with long-wave light without a filter, or at normally illuminated objects through a long-wave filter.

Henning considers that both the red and yellow droplets share in this supposed effect, and explains the red droplets of turtles as primarily for di-aquatic vision and secondarily for vision through long air pathways. He contends that even land turtles pay much attention to water and that the vital activities of turtles are largely carried on in morning twilight conditions[20], and are of such nature as to require sharp distant vision. Turtles, he says, do indeed have much better distant vision than other kinds of reptiles.

This author considers the macular pigment of man to have the function of absorbing blue haze and thus sharpening the image as does the yellow filter of a camera; it is because of the macular pigment, he claims, that we see better (?) through mist with central fixation than with paracentral (this, however is most doubtful, for the concentration of cones is not at all the same in the two cases).

Henning's hypothetical paleobiological explanation of the droplet-colour assortments of the various vertebrate groups must be received with great caution[21], and his demonstration of the inability of birds to "home" when provided with blue goggles has been shown to be meaningless by Erhard (1924). His most severe critic, however, is Honigmann (1921), whose objections have been widely quoted by authors who have not perceived certain fallacies in them.

[20] When the sunlight reaching the animal is reddened by the long air pathway which it has traversed.

[21] And compare the exactly antithetical paleobiological theory of Hulburt (1926).

Honigmann thinks, like Henning, that long waves penetrate mists best, but ridicules the idea that a practical benefit would be derived from a red filter. He contends that Henning implies that a red glass produces an actual objective increase in the amount of red light (Henning does, actually, confuse scattering with fluorescence and states that when white light passes through fog there is an objective increase of its red content). Mist, Honigmann claims, cuts out some short-wave light and the filter cuts out some more, but any benefit to be obtained must come from the elimination of the chromatic aberration due to the short waves. Honigmann says that if chromatic aberration is detrimental we should see better through mist than through clear air, for the mist cuts out the rays most responsible for the detrimental effect. He thus takes no account of the difference in total illumination, nor does he realize that short-wave light is not *per se* undesirable—it is only when scattered short-wave light is mixed with more direct long-wave rays that it produces that blurring which is not due to chromatic aberration, and chromatic aberration itself is detrimental to vision only because both short-wave and long-wave lights are entering the eye.

Erhard (1924), while not satisfied with any theory, supports Henning from his own experience with the value of yellow goggles in improving detail, especially in snowscapes in mountainous country. He states that the German Navy uses yellow filters in telescopic instruments in misty weather, and that photography shows the value of yellow filters even in the clearest weather. Yellow filters improve vision, Erhard thinks, chiefly by reducing dazzle and by enhancing contrast in flat[22] fields of view.

The situation may now seem confusing to the reader. There can be no doubt of the value of colour-filters in photography and vision, but several questions arise: Under just what conditions are filters of various colours useful? To what physical phenomena do they owe their efficacy? Is any extrinsic filter of practical value in *human* vision, under any natural circumstances? It may seem that an affirmative answer to the last question is pre-requisite to the acceptance of an interpretation of *intra-ocular* filters in these general terms, but it will appear shortly that such is not strictly the case. The possible effects of a yellow filter are as follows:—

1.—*To increase visual acuity by reducing chromatic aberration.* —Because of their different refrangibility the various wave-lengths are brought to independent foci by an uncorrected lens system. The violet rays are focussed nearer, the longer wave-lengths progressively further from the lens. Moreover, the dispersion is not uniform, but greatest in the violet and progressively less toward

[22] In the photographic sense.

the red; thus the shorter wave-lengths contribute more to the thickness of the total image. Any approach toward monochromasy will improve matters, but if only a part of the spectrum is to be absorbed, it is logical that the short-wave end should be that part. Such absorption is accomplished by a yellow filter, and the effect will be manifest without regard to the character of the medium looked through[23].

Luckiesch (1911) found that with monochromatic lights of equal subjective brightness the maximum visual acuity was obtained with yellow (λ5800); short wave-lengths gave lower acuity, as did the long end of the spectrum. While this phenomenon has nothing to do with chromatic aberration it points to a fortunate multiple coincidence: a yellow filter will reduce chromatic aberration considerably while transmitting maximally the very wave-lengths to which the retina is most sensitive, which, *per se*, yield the highest visual acuity. Furthermore, the yellow filter reduces general illumination minimally since the shorter wave-lengths have the lowest energy content; hence a minimum of brightness is sacrificed.

It apparently needs emphasis (for Honigmann, at least, has overlooked the point) that short wave-lengths are not in themselves particularly detrimental to visual acuity, but only when intermingled with longer wave-lengths. As Erhard has pointed out in rather simpler terms, the predominance of short-wave rays in nocturnal illumination make it a positive optical fault for scotopic visual cells to possess an absorbent for such rays. Hence we find that animals whose yellow filters are homogeneous are restricted to purely diurnal vision. Only the oil-droplet mechanism, with its potentiality of having only *some* receptors provided with filters, can succeed in nocturnal animals whose eyes are important to them. Thus some owls have *some* coloured droplets, which fact reflects their imperfect nocturnality (see Erhard, 1924). Other animals which have oil-droplets in *all* of their visual cells must of necessity abandon all pigmentation thereof in order to become perfectly nocturnal (witness *Xantusia* and *Heloderma*).

2.—*To promote comfort by the reduction of glare and dazzle.*—This is a more or less "intangible" factor but none the less real. The effect of a filter upon dazzle is not proportional (unless it be a "smoked" one) to its total absorption coefficient, since the hue-sensitivity curve of the photopic human eye is sharply peaked in

[23] Luckiesch (1911) has called attention to an interesting point. A concave spectacle placed before an eye reduces chromatic aberration by approximating the violet and red foci. Such a lens, together with the ocular media, tends to form an achromatic system. Reduction of the effects of chromatic aberration, in this manner, may possibly occur in lampreys and snakes—provided of course that the refractive indices of the lens, cornea, "Brille," and the curvatures of the latter are suitable.

the yellow region—and we have noted also that the birds are especially sensitive to long visible wave-lengths. A yellow filter would, therefore, have less effect upon dazzle than a red one of equal density, but perhaps represents a compromise since a red filter would greatly alter chromatic values and might absorb too much photic energy under average conditions.

Scattered light, in nature, is largely of short wave-lengths; if sufficiently bright a true glare results, which a yellow filter will obviously minimize.

3.—*The enhancement of detail by the absorption of "blue haze."* —In photography, even with apochromatic lenses, a yellow filter is still found valuable for increasing detail. This effect, present of course also in vision, is due to the absorption of the scattered, unfocussable blue light which pervades the atmosphere and tints the sky. Even when insufficiently bright to bring about glare, this light is responsible for a blurring of the image.

4.—*The enhancement of contrast* has several phases. The elimination of the blue of the sky increases the visibility of objects seen against that background. Most filter-bearing vertebrates have much to fear from aerial foes, and arboreal forms such as the squirrels must welcome any increase in the visibility of the slender branches toward which they leap. These same twigs must be clearly seen and avoided by birds flying among them.

More general contrast-producing effects of yellow filters have been emphasized by Erhard. We would point out still another property peculiar to the oil-droplet mosaic and resident in the arrangement of the coloured droplets: the predominance of yellow droplets in the ventral portion ("yellow field") of the pigeon's retina is especially convenient for the production of contrast against the sky. The heavy concentration of red droplets in the dorsal quadrant ("red field") perhaps enhances the visibility of objects seen from the air against the green surface of the earth. While this situation is by no means widespread among birds, as is frequently assumed, such regional differences in the oil-droplet pattern have their only obvious interpretation in terms of contrast production.

The non-oil-droplet types of yellow intra-ocular filters must also perform the above functions in greater or lesser degrees. The very fact that a *red* filter is relatively uncommon indicates that its special functions are secondary and less widely demanded. We will shortly consider what those functions may be.

The filter-bearing vertebrate must compromise between the advantages of some differential absorption and the disadvantage of cutting out so much light as to dim its vision appreciably.

The level at which the balance is struck will depend upon the habits of the animal. Thus the "sun-worshipping" prairie-dog, *Cynomys ludovicianus*, and ground-squirrel, *Citellus t. tridecemlineatus*, have deeply and equally pigmented lenses. The chipmunk (*Tamias striatus lysteri*), the red (*Sciurus hudsonicus loquax*) and fox-squirrels (*S. niger rufiventer*) and the woodchuck (*Marmota monax rufescens*), all of which[24] favour light timber or the edges of woods, have lenses less deeply coloured. The grey-squirrel (*S. carolinensis leucotis*), which prefers heavy timber, has a still paler lens; and the lens of the (nocturnal) flying-squirel (*Glaucomys v. volans*) is perfectly colourless. The snakes exhibit the same correlation (*see* Walls, 1931), but here the degree of pigmentation also shows a relation to the activeness of the species—possibly a coincidence, but we think meaningful; a swift animal, other things being equal, naturally needs keener vision than does a sluggish relative.

Because only a rather deeply coloured filter is found to improve human vision appreciably under certain experimental conditions, some may be led to question the efficacy of natural filters (on the ground that they are "too pale") in producing any or all of the above effects to a really valuable extent. Two points must be kept in mind when debating this matter. In the first place, the human eye is *already* provided with an intrinsic yellow-filter system[25]. We cannot judge how much our vision would suffer if this system were not present, and we must not expect a pale extra-ocular filter to add much, for it constitutes a minor part of the total absorbent complex. As is shown clearly by cone-to-rod ratios, man is not the most strictly diurnal of the primates; merely because human vision can be improved in bright light by an extra-ocular yellow filter, that is no indication that the human macula lutea is "imperfect" as an aid to vision and that therefore it must have some function other than those proposed here for natural yellow filters in general. Any such conclusion must be held strictly in abeyance until the extent of macular pigmentation in the more cone-rich primates has been learned.

Referring to their previous work (1925) in which a thin layer of saturated potassium bichromate solution was found to increase visual acuity when employed as a filter, Luckiesch and Moss (1931) say:—

"It was found that no great increase in visual acuity resulted from the elimination of the light of short wave-lengths. In general,

[24] The lenses of these four forms are all matched by a 2 mm. layer of Noviol "O" glass (see Walls, 1931). The American Optical Company informs us that this glass transmits 79 per cent. of the total energy of the visible. This should be somewhere near the value for the animal lenses.

[25] Which includes not only the macular pigment and the capillary network, but also the yellow colouration of the lens—a senile change, but one which is so usual in persons past thirty years of age as almost to deserve to be considered physiological.

the increase in visual acuity approximately compensated for the decrease due to lesser intensity of illumination as the filter was increased in density. This not only tends to establish the unimportance of spectral character in seeing colorless objects, but also shows that there is no appreciable advantage in eliminating the blue end of the spectrum."[26]

These remarks apply to human vision under indoor conditions, but it is not to be supposed that they would hold true of an eye deprived of its intrinsic filters. Luckiesch's claim that ". . . the use of colored lenses without increasing the candle-power of the light-source results in a net loss in the ability to see" holds good for ordinary artificial lights, but under the much brighter *outdoor* conditions the loss of intensity brought about by even a deeply coloured filter is no sacrifice, and the benefits of the filter are fully enjoyed[27].

That extra-ocular colour-filters are of very real value in human vision under natural outdoor conditions is shown by the experience of the United States Navy. Mr. Laurence Radford of the Bureau of Ordnance, to whom we applied for information, replied as follows:—

"The Navy uses both red and yellow color filters in optical instruments. Both are made of Corning Glass. The red cuts quite sharply at about λ6000-6200 and the yellow at about λ5100-5300[28]. These filters are used because much experience has shown that they are helpful, and the particular filters selected were chosen after considerable study, both experimental and theoretical.

"In my opinion these filters are effective for our purposes because they reduce glare due to scattered light and minimize the effects of the chromatic aberration of the eye, and for these reasons almost exclusively. These two effects are produced more intensively by red than by yellow filters, *i.e.*, the amount of scattered light transmitted by the red is much less than by the yellow because the latter transmits the green; and with the red filter the effect of chromatic aberration is practically eliminated. But there are conditions when the red filter cannot be used effectively, perhaps because of insufficient intensity of illumination, or perhaps because

[26] They say: "Certainly (chromatic aberration) is a defect of vision but, excepting in special cases, it is of little or no importance"; but *cf.* Hildreth (1932)—the linear chromatic aberration of the human eye has been variously computed as from one to four dioptres.

[27] Coblentz (1932) found that the darker shades of tinted commercial optical glasses increased visibility outdoors, though he considers the effect solely due to the absorption of blue haze. Coblentz claims that a filter must transmit only a *narrow* band of wavelengths in order to increase visual acuity through an effect on chromatic aberration; we cannot agree.

[28] These figures are intriguingly close to those reported for the oil-droplets of the fowl by Roaf (1929*a*, *b*), who found that the red droplet absorbs up to *ca.* λ5800-5900, the yellow up to λ5150-5250.

it would reduce the color contrast. Hence the two colors, giving us essentially the choice of two degrees of the same effect."

Further evidence of the value of yellow filters in human vision is afforded by rifle marksmen, many of whom have long been convinced that such filters improve definition. Mr. F. H. Edmonds, a Washington optician who has experimented with filtering goggles for Army rifle teams, tells us that his experience indicates that Noviol "C" glass effects a maximal net improvement in visual acuity. Many marksmen have particular preferences, however; a former national champion informed us that he favoured an amber (Hallauer 63) glass as it eliminated headache due to the dazzle and glare, but had not chosen the glass for its effect on visual acuity as his unaided sight was exceptionally keen.

Still another, purely aesthetic application of yellow glasses is in landscape viewing (Laurance, 1920).

The functions of red filters, as exemplified by the red oil-droplet, are not so simply expressible. If the intensity of illumination is sufficiently high, or/and the sensitivity of the retina is especially great for long wave-lengths, the red droplet will perform—even better—the functions of combating chromatic aberration, blue haze, and dazzle ordinarily cared for by yellow filters. On the other hand, contrast effects will be hindered rather than promoted, due to the limitation of perceptible chromatic values, and this alteration will also be detrimental to colour vision in its ordinary sense.

As suggested by Mr. Radford's statements (*v.s.*), the red and yellow oil-droplets may be considered to afford two different degrees of the same effect—the two filters being only interchangeable in a telescope, but simultaneously available in the eye of the bird or turtle.

Without going further we can now understand the exclusion of red droplets from the avian fovea. The bird cannot permit such alteration of colour values and cannot chance a detrimental dimming of vision in that area. The extra-foveal duplicity of the coloured droplet mosaic affords a maximal benefit over a considerable range of intensity—the yellow cones playing the more important part in ordinary illuminations and the red ones coming into play especially in very bright sunlight.

Analysis of the behaviour and environment of the diurnal birds points at once to a special situation in which a red filter becomes of advantage. Birds are markedly matutinal, and in the twilight period in which their activities are concentrated there is a pronounced reddening of the incident sunlight due to Rayleigh scattering in its greatly lengthened path. The red droplets of the

birds are especially valuable at this time; they undergo a change of function as the sunlight becomes brighter and whiter, taking on then the function of supplementing the action of the yellow droplets to a degree dependent on the brightness of the sunlight.

Indirect evidence of this special matutinal function is afforded by the situation in the diurnal raptorial birds. Hawks and their allies are incapable of their typical high flights and soaring until lifting air currents have been produced by the rising sun. These prey-seeking activities, placing the heaviest demand upon the keenness of sight, do not commence until about 9 a.m. sun time, when the ruddy glow of early morning is gone. This, we believe, accounts for the relatively very low proportion of red droplets in such birds (see Erhard, 1924)[29].

Turning for a moment to the turtles let us consider the questions posed by their red droplets. The majority of turtles are partly or wholly aquatic; if we assume for the moment that their red droplets are an adaptation for underwater vision it may be reasonably asked why red filters are lacking in fishes. The pure-cone character of most chelonian retinae, together with the many points of superiority in the turtle's ocular anatomy, make it probable that minor refinements of vision would be worth while in this group. But in the fishes the coarseness of the cone mosaic and the size of the cones precludes the attainment of a really high visual acuity by the use of any accessory device. Moreover, the use of any but an *oil-droplet* filter makes necessary the choice of a single "all-purpose" colour, and the colour evolved will naturally be the one with the widest usefulness, *i.e.*, yellow.

It has been claimed that human underwater vision is improved by an extrinsic red filter. We have been unable to find any special physical reason for such an effect and can only suggest that, if the intensity is very high, any benefit would derive from the selfsame properties such filters possess in aerial vision.

Only two possible factors could endow a red filter with advantages *peculiar* to underwater use thereof. If Rayleigh scattering were produced in natural waters by minute (*i.e.*, $<.75\mu$) particles, the red rays would be transmitted in the best focussable condition and a red filter would then be needed to deal with the scattered zone of the spectrum, which would then include longer wave-lengths than blue. If such scattering occurred, however, objects seen through water would appear ruddy as they do through a smoke haze—and such is not the case. The blue colour of

[29] Relatively few red droplets are present in woodpeckers, also (Erhard); these birds are notoriously poor fliers and do most of their seeing at very close range, where a red filter would be of no value. In the one woodpecker in which we were able to study the fresh fovea (*Dryobates pubescens medianus*), the fovea was very shallow. The paucity of red droplets in swifts, etc. (see Krause, 1894) is probably related to their crepuscularity.

deep water, unlike that of smoke and the sky, is an intrinsic colour.

If red rays suffered much less extinction in water than others there might be benefit from a red filter. Hulburt (1926) claimed that yellow filters were transmitted best through 40 metres of sea water and there is abundant evidence that the shortest rays are the last to be extinguished at great depths; but it has never been claimed that red rays are transmitted best to any level. They are the *first* visible rays to be extinguished, the shorter and shorter wave-lengths penetrating deeper and deeper until only violet (Grein, 1912) or blue (Hulburt, 1932) is left.

Henning has stated that human vision through *turbid* aqueous media is aided by a red filter. Natural waters, however, are rarely if ever rendered turbid in a way which would produce the Rayleigh effect. We have consulted the two American manufacturers of diving equipment; neither knew of any experimental evidence of a beneficial effect of any type of filter in underwater vision. Reighard (1907) employed yellow filters in diaquatic photography, but was not sure that they were really helpful. The "blue translucence" which, according to Reighard, envelops objects seen horizontally under water at distances greater than a few feet, might be combated with a yellow filter; but any benefit would be due chiefly to contrast effects. At considerable depth, under a very bright sun, a pale *blue* filter[30] might even be helpful —*but never a red one.*

If the red droplets of turtles were primarily adaptive to underwater vision, such droplets would be unnecessary, even detrimental, to strictly terrestrial turtles. But we have found a desert turtle, *Gopherus polyphemus,* to have as well-developed ruby droplets as any aquatic form. *Chelydra serpentina,* also, has numerous large red and orange droplets though this species is a mud-loving scavenger and has little need for good vision through water. If the relatively recent *Xantusia* has been able to decolourize its droplets, and the still more recent snakes, during their early evolution, were able to discard them completely, it would seem that such ancient forms as the land turtles must have had ample time to get rid of red pigment if the latter became useless, or worse, when the desert habitat was adopted.

Again, if the red droplets of turtles were of special value under water, an exceptionally high *proportion* of such droplets would be expected in diving birds. Erhard (1924) found, indeed, that in the fundus of a European kingfisher 60 *per cent.* of all the droplets were red, as compared with an average of only 20 *per cent.* for five other miscellaneous passerine species. A duck

[30] Reighard mentions that Boutan once adopted blue filters in his underwater photographic work, but later abandoned them.

(*Nycora fuligula*) and a heron (*Ardea c. cinerea*), however, each had only 20 per cent. reds. The European water ouzel showed 24 per cent. red droplets. This bird has no structural adaptations for aquatic activity, whereas the kingfisher is beautifully adapted for plunging[31]. Thus the low number of red droplets in *Cinclus* might seem a part of the general lack of aquatic specialization—were it not for the similar low numbers in *Nycora* and *Ardea*. It appears safe to say that the "extra" red droplets in *Alcedo* are *not* adaptive to underwater vision; their probable meaning will be considered later.

It is widely supposed that red light penetrates fog differentially well. Unless smoke is present, however, there is no such effect (see Granath and Hulburt, 1929). Red light would get through fog better than other visible wave-lengths if the water particles were less than 0.75μ in diameter, but this limit is exceeded by even the smallest natural fog particles (Houghton, 1931, 1932). The reddening of horizontal sunlight is due to Rayleigh scattering by particles of molecular size or but little larger, and no such reddening occurs in clean, true mists or fogs. There is no possibility that red oil-droplets aid vision through true mist, as Henning claims[32].

The red droplets of turtles are certainly of no value in mist, and of less value under water than in clear air. The Navy's experience affords, we believe, the clue to their function:

In clear weather glare *over water* is especially severe due to reflection from the surface. The turtles, unlike other diurnal vertebrates, must do most of their seeing over water with the eyes at little or no height above it. Their problem is thus essentially identical with that of the Navy—and their red and yellow (or orange) droplets equip them to meet it in the same way, with the advantage that the turtle's two filters are interchanged for him automatically. Even *Chelydra* basks and needs its red droplets at such times. The retention of the red droplets by desert tortoises is now comprehensible, for they have a glare problem which most terrestrial animals never encounter. So also with the kingfisher, whose red droplets must be capable of performing the *extra* function of defeating the glare which interferes

31 And Kolmer (1924) has noted gross features of the eye itself, in *Alcedo a. attis*, which he considers adaptive to diaquatic vision.

32 In England the use of yellow fronts on automobile "fog lamps" and of temporary headlight colourants, such as the proprietary "Mortifog," is fairly common. The coloured light-beam produced owes its fog "penetrating" power solely to its *lowered intensity*. The glare from a brilliant beam in fog results in lower visibility than is obtained with a downward-directed beam of less intensity. Many American motorists prefer to use their auxiliary dim lights when driving in fog.

In this connection, note a statement in Mr. Radford's letter to us: "We do not, of course, expect to see through fog with either filter for . . . fog particles are too large to show selective scattering in the visible region."

with the clear perception of the prey from the bird's observation station a few feet above the surface.

We have stressed the functional divorce of the distinct oil-droplet colours. The average (*e.g.*, human) rod-and-cone retina (extra-foveally), is spoken of as *duplex*; it is perhaps logical to speak of the droplet-bearing retina (again, extra-foveally) as *multiplex* in much the same sense, for the independent sets of similar cones are each of maximum value under some particular set of conditions[33]. The red, yellow, colourless, etc., cones, interpreted by a "multiplicity theory," are seen to be relatively independent mechanisms just as the simpler cone- and rod-mechanisms of droplet-free vertebrates are independent. External conditions will not be optimum for more than one mechanism of a "multiplex" retina at any one time—which is true also of the "duplex" retina. The mosaic of any one colour of cones, however, is sufficiently fine-grained[34] to afford a minimal visual angle comparable with that of the extra-foveal cone mosaic of duplex retinae. The colourless cones become functionally prominent in dim diurnal illuminations and afford a transition between the coloured bright light mechanisms and the rod-system. Even in bright light colourless cones will naturally aid in preserving chromatic values which the pigmented cones tend to suppress.

We have so far said nothing as to the *orange* droplets which are prominent in turtles and occur also, along with reds and pure yellows, in birds. The more distinct categories of droplets found in a given retina, the more the colour-vision theory *seems* to be strengthened, but we interpret the orange droplet as simply a transitional mechanism bridging the functional gap between the red and yellow systems.

We can offer no explanation as to why these three types of oil-droplets are so *distinct* as to colour, size, height above the external

[33] Blässer (1926) considers the partial blue-blindness of the fowl to be due to "additive" absorption in the red and yellow droplets. He implies that there is some neurological mechanism which brings about the same result as though the red and yellow droplets occurred in tandem in a single cone. Hess and others speak of the bird and turtle as "seeing the world as we would if we looked through an orange glass"—assuming that the actions of the red and yellow droplets are in some way blended so as to simulate the effect of a homogeneous intermediate (*i.e.*, orange) screen. We can imagine no such neurological mechanism as this view demands. The most intimate relation possible for two differently-coloured single cones is to be in synapsis with the same bipolar neuron. The result would be analogous to illuminating a room through two windows of different colours—*not* a single window made of two superimposed panes of different colours. Blässer, Hess *et al.* have ignored the difference in the laws of hue- and of pigment-mixture; they are perhaps misled by the manner in which orange is produced by the red and yellow dots of a multicolour process illustration. Rochon-Duvigneaud (1929), at least, has clearly perceived this fallacy.

[34] Diurnal birds have very few rods and most turtles none at all. A pair of adjacent cones containing oil-droplets of the same colour are thus at least as close together as two adjacent extra-macular human cones. This does not hold, of course, in cases where a given type of droplet has lost its importance and degenerated, *e.g.*, the few widely scattered red droplets of the swifts, etc.

limiting membrane, etc.; the cones which differ as to colour of droplet differ also in other respects, and this differentiation is a mystery at the present time. But "intermediate" types of visual cells almost never occur along with the distinct cones and rods of duplex retinae, which, in similar fashion, replace each other functionally as illumination-conditions change. A smooth functional replacement of one mechanism by another does not then necessitate a structural intergrading of the two mechanisms. Were it not for the very distinctness of oil-droplet types the colour-vision theory would not seem so plausible, but the distinctness does not constitute an obstacle to the "multiplicity" theory presented here.

Many investigators of bird retinae have remarked on the fact (confirmed by our own observations) that an orange droplet is very frequently paired with a red one, the two being so close together as to make it seem that they are in the two members of a double cone[35]. The meaning of this pairing is not clear; but that the red and orange droplets are of most importance (apart from early morning) under the brightest conditions, the yellows of chief importance under more ordinary outdoor illuminations, is indicated by the observation of Kühne (1882, p. 107), that each red-orange pair of cones is surrounded by heavy retinal pigment, while less of the latter is present in the neighbourhood of the cones which contain yellow oil.

The occurrence in a few birds, as recorded by others and noted by us in the Flicker, of some yellowish droplets, which are really more green than yellow, or of a separate set of truly green droplets, is wholly mysterious to the writers. Such droplets probably pass a band of wave-lengths practically as wide as do the pure yellow ones, but curtailed somewhat at the red end. While green droplets fit nicely into the colour-vision theory of oil-droplet function, they are exceedingly rare and have no place in our own theory; we must leave their interpretation to a wiser future.

To sum up: Any colour-filter is worse than useless in scotopic vision. Natural yellow filters in general, including all yellow and orange oil-droplets whether found alone or combined with red ones, have a quadruple beneficial effect on photopic vision under average outdoor conditions. They do not help to *endow* the animals with colour vision—they *modify* it. They are not designed to equalize the actinic power of wave-lengths, nor do they protect the visual cell outer segments from ultra-violet light. None of the pigments concerned can be considered photochemical substances comparable with visual purple, etc.

[35] This is probably not the case, however; sectioned material rarely if ever reveals a double cone *both* cells of which contain oil-droplets.

Red oil-droplets perform, incidentally, most of the functions of yellow filters—even better than the latter when the objective light intensity is very high, but introduce an undesirable curtailment of the range of the subjective chromatic spectrum, and become inefficient in "comfortable" illuminations except where the amount of scattered medium-wave light is great, as at the twilight periods. For these reasons they are never found alone, but always accompanied by large numbers of paler droplets which bear the brunt of the work of vision under ordinary conditions. The primary importance of red droplets, in birds, is in sharpening vision in the reddened illumination (with its accompaniment of scattered violet, blue, and green light) of their favourite matutinal period of great activity. In turtles (and the kingfisher?) their primary function is to reduce the excessive glare which interferes with sharp vision over water. A red oil-droplet is of no value in natural mist or under natural waters.

Those diurnal vertebrates which rely upon lenticular, corneal, macular, and capillary filters must of necessity choose a single optimum colour and density, and accept a resultant limitation of those activities in which their visual capacities are important. The oil-droplet type of filter, however, permits of the development of a functionally multiplex photopic apparatus, with a resultant wider range of adaptation to varying illumination conditions. Because many cones would not be maximally efficient under any one static set of conditions, only very cone-rich retinae can afford to evolve a multiplex oil-droplet mosaic—and it is in such retinae that the multiplex system finds its highest expression.

To be continued.

THE CILIARY MUSCLE AND DESCEMET'S MEMBRANE

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SIR ARTHUR THOMSON in *The Ophthalmoscope* Vol. IX, 1911, described the action of the ciliary muscle on the scleral spur, at the angle of the anterior chamber, with a pump-like effect. It is probably a tribute to his work that to-day it is generally taught that the anterior attachment of the ciliary muscle is to the scleral spur.

(*Vide*: Cunningham's "Anatomy"; Gray's "Anatomy"; Buchanan—"Manual of Anatomy"; Duke-Elder—"Text-book of Ophthalmology I.")

Now a study of the histology of the angle of the anterior chamber does not satisfy one that the anterior attachment of the ciliary muscle is to the posterior border of the scleral spur.

The *ciliary muscle* anteriorly ends in connective tissue. Much of this tissue is attached to the posterior border of the scleral spur, but a good deal passes straight forwards, avoiding the scleral spur altogether, towards the "end of Descemet's membrane."

From the anterior border of the scleral spur trabeculae pass forward to the "end of Descemet's membrane" and to the inner corneal lamellae.

Most authors admit freely that there are two separate sets of trabeculae at the angle of the anterior chamber medial to Schlemm's Canal, viz:—

(1) *Scleral trabeculae* running to the scleral spur, and
(2) *Uveal trabeculae* passing directly to the ciliary muscle.

(Henderson, Parsons, Salzmann, Fuchs, Rauber-Kopsch, Lyle and de Souza).

As regards the posterior attachment of the ciliary muscle, there is almost universal agreement that the posterior attachment is to the sclera of the posterior segment of the eye, although the choroid is pulled upon and moved forwards and backwards to some extent when the ciliary muscle contracts and relaxes.

Were the posterior attachment of the ciliary muscle merely to the choroid this vascular organ would be torn by the pull exerted on it.

The ciliary muscle exhibits a diversity of functions that must be well-nigh unique. Its work as regards the accommodation of the eye is sufficiently appreciated. It is probably worth while, however, to refer to the striking analogy between its posterior and anterior attachments.

Posteriorly, the ciliary muscle

(1) is attached *directly* to the whole of the posterior portion of the eye.

(2) *A neighbouring tissue is interposed* between the muscle and its ultimate attachment, viz., the choroid.

(3) The choroid has sufficient connection with the fibres of the posterior attachment to cause its anterior portion to move with the fibres, and to dilate and to collapse as the ciliary muscle contracts and relaxes—a matter of the greatest importance to the *vascular circulation* of the eye.

Anteriorly, the ciliary muscle

(1) is attached *directly,* according to our view, to the whole of the cornea.

(2) A *neighbouring tissue is interposed* between the muscle and its ultimate attachment, viz., the scleral spur.

(3) The scleral spur has sufficient connection with the fibres of the anterior attachment to cause its anterior portion to move with

Two photographs showing the structures at the angle of the Anterior Chamber.

the fibres as the ciliary muscle contracts and relaxes, thereby causing the canal of Schlemm to dilate and to collapse—a matter of the greatest importance to the *intra-ocular fluid circulation* of the eye, especially in cases of raised intra-ocular tension.

We would suggest then that the anterior attachment of the ciliary muscle should *not* be regarded as being to the scleral spur—any more than the posterior attachment is now regarded as being to the choroid. Were the ciliary muscle attached anteriorly merely to the scleral spur, without the support of the scleral trabeculae, we would expect that the scleral spur would probably be torn, just as in the case of the choroid, when the muscle contracts.

In Collins and Mayou "Pathology and Bacteriology of the Eye," p. 347, a similar condition is actually described where the ciliary muscle loses its most fixed point of attachment and the ciliary body is displaced backwards when the ligamentum pectinatum is ruptured.

More accurately the whole of the cornea should be regarded as being the anterior attachment of the ciliary muscle.

Descemet's Membrane is described by Salzmann as being a typical glass membrane—a highly refractile structureless homogeneous membrane of great firmness and elasticity. Descemet's membrane is 5 – 7μ thick in the centre part. Towards the angle of the chamber it increases to 8 – 10μ in thickness.

Salzmann further describes the thickened end of Descemet's membrane as breaking up and splaying out to help form the trabeculae.

Gray's "Anatomy" states definitely "the triangular mass of trabecular tissue . . .. is continuous with the posterior elastic lamina of the cornea."

Parsons agrees with this view in his "Diseases of the Eye."

Fuchs in his text book (15th Edition) regards Descemet's membrane as being a part of the uveal tract.

Collins and Mayou (p. 78) state that "the fibres of the ligamentum pectinatum stain and react in precisely the same way as the hyaline layer of Descemet's membrane and, like it, are probably the product of the cells which ultimately line them."

In view of the evidence quoted above together with the description of the histology of the parts under discussion the question arises whether Descemet's membrane should not be regarded as an anterior tendon of the ciliary muscle. That it could be a "tendon" modified for the optical purposes of the eye, just as the opaque sclera is modified to become the clear transparent cornea, is not incompatible with its nature, structure, position, proportions, connections, histological staining reactions, mesodermal origin, and embryological development.

In considering this question it should be remembered that the eye is capable of rude departures from recognised histological rules—we mention two of these—the dilator muscle arising from ectodermal tissue, and the growth throughout life of the lens, an ectodermal tissue, without ever casting off any of its cells.

I am indebted to Mr. H. B. Stallard for his kindness in allowing me to make free use of the pathological laboratory at Moorfields.

THE DIAGNOSIS OF IRIDO-CILIARY TUBERCULOSIS

BY

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BEFORE entering upon discussion of the report on the direct and differential diagnosis of tuberculosis of the iris and ciliary body, I desire to present this problem in a few words as illuminated by the papers which I have had the honour of classifying and abstracting for your information.

I.—Ocular Tuberculosis is a Secondary Lesion supposedly due to Superinfection

Publication of the first case of iridian tuberculosis by Gradenigo and Richetti, in 1867, was immediately followed by a discussion on the pathogenesis which has only recently been really closed. It was necessary to determine whether irido-ciliary tuberculosis was a primary or a secondary effect.

Many collected cases seemed to indicate that this affection was primary. Denig, for example, collected, in 1885, 38 cases of localized ocular tuberculosis not having any evident previous history of tuberculosis. With these cases he compared systematic examination of 60 cases of pulmonary tuberculosis, 90 cases of bone tuberculosis, 20 cases of glandular tuberculosis and 20 cases of various types of tuberculosis. In all of these comparative cases, only five showed ocular metastasis.

In contrast with this finding, however, was the opinion stated by de Wecker, in France, Leber, in Germany, and Fuchs, in Austria,

* Introduction to discussion of my report on the direct and differential diagnosis of tuberculosis of the iris and ciliary body, International Congress on Ophthalmology, Madrid, April 16, 1933. *Cf.* "Tuberculosis of the Iris and Ciliary Body," published by G. Doin & Company, Paris, 1933.

and based upon clinical evidence, that deep ocular tuberculosis originated from some other point in the organism and that it was consequently *secondary*. In 1905, differences in opinion were so marked that Schmidt-Rimpler wrote: "I confess that I do not understand why Fuchs and Leber disagree with Michel in believing that tuberculosis of the iris is always secondary and dependent upon a primary site of tuberculosis. Why may not the bacilli of tuberculosis reach the iris by way of the blood as well as they may reach bones and lymphatics, producing there the first visible signs of the affection?"

This teaching became progressively affirmed by experimental study and agrees with the present views universally held in phthisiology, namely, that ***tuberculosis of the uveal tract arises from a deeper site not at first recognized.***

Tuberculous infection is thus conveyed to the uveal tract through the blood, as believed by Leber. The first experimental demonstration of the fact was presented by Felix Lagrange, in 1898. Injecting an emulsion of tubercle bacilli into the carotid arteries of ten rabbits, he produced tuberculous infection of the uveal tract in two cases. These studies of his have established the basis of our present pathogenic knowledge on the question. They were repeated, verified and completed nine years later by Stock and Daels (1907) and mark one of the historic stages in scientific progress, since they show the *manner* in which tuberculous infection reaches the uveal tract, by a bacillaemic or a septicaemic process. I believe that it is now possible to determine from Aschoff's work on the reticulo-endothelial system *why* the uveal tract constitutes a favourable site for the formation of tubercles.

While the work by Felix Lagrange, Daels and Stock concerning the mechanism of localization of tuberculosis in the uveal tract proves its haemosporic origin, it was evident that these writers obtained only miliary lesions not possessing the characters of uveal tuberculosis commonly present clinically. For this reason I attempted to obtain, in 1923, experimental specimens more like those occurring in human pathology. I succeeded in this endeavour by inoculating the uveal tract from animals previously rendered tuberculous. My results formed a contrast with the local reactions following primary inoculation and with the lesions obtained with superinfection, that is, by inoculating with tuberculous products the uveal tract of animals previously rendered tuberculous. These studies showed that it is necessary to use animals previously rendered allergic in order to reproduce tuberculous lesions of the uveal tract which resemble those encountered clinically.

Onward from this point, ophthalmological cases accumulating for nearly fifty years may be interpreted according to the principles of general pathology which, especially influenced by the work of

Ranke, have shown that the wide variations occurring in tuberculous lesions are due to variations in allergy. Even if these various data be considered only from the diagnostic viewpoint, a fundamental idea is derived from them, namely, that irido-ciliary tuberculosis, even when occurring as an isolated sign in an organism appearing to harbour no other localization of the tuberculous infection, is derived from a primary site, which demands initial study and examination.

II.—Diagnosis requires initial proof of the presence of Primary Infection

If it be desired to state just when it was perceived that ocular tuberculosis develops in individuals not presenting other visceral signs of progressive tuberculosis, it suffices to reconsider the history of the pathogenic controversy alluded to by Schmidt-Rimpler and entered into by such men as Fuchs, Leber, Parinaud or von Michel. Clinicians of such eminence believed that tuberculosis may be primary in the irido-ciliary region because ocular tuberculosis rarely co-exists with distinct signs of previous tuberculous infection.

(*a*) Pulmonary signs.—In this report I have reviewed the history of the cases accumulated on this point, and, like Rist, have been obliged to conclude that "pulmonary forms of tuberculosis, on the one hand, and extra-pulmonary manifestations, on the other, form two distinct groups, since they present more than one contrasting character and exhibit a singular sort of balance."

Though extra-pulmonary forms are characterized by being clinically primary, though their activity is in nowise parallel to that of pulmonary lesions, and though it is vain to seek concomitant pulmonary lesions for the diagnosis of the extra-pulmonary forms, are there no guiding or orienting points in the general examination of a case which should be learned and sought for?

J. Meller seeks pulmonary signs in every case of ocular tuberculosis, and stresses the frequency with which recurrent pleuritis is encountered. Rist and most contemporary writers consider that ocular tuberculosis is always secondary to a pre-existing pulmonary site of infection, but if the latter produces no noticeable signs, this "chancre of primary inoculation" may always be shown by careful X-ray examination. No better description is possible than that given by Rist and Ribadeau-Dumas, who say, "these calcified vestiges of cured primary tuberculous inoculation occur in the radiograms of healthy children or adults. They usually occur at the base of a lobe, often in the prolongation of a bronchial twig, sometimes very near the pleura in the axillary region and rarely at the pulmonary apices. Whenever such an intra-parenchymatous

calcification is discovered, a homologous calcification may always be found in the pulmonary hilum, and consequently in a gland."

(*b*) Cardio-vascular signs.—It goes without saying that other regions of the organism (digestive tract, bones, joints and lymphatic system) should also be thoroughly examined, but I desire to stress the importance which I personally attach to study of the cardio-vascular system. Tuberculous infection may attack this system as it may invade any other structure, especially producing tuberculous cardiopathies. The latter, however, are not important from our present viewpoint, for we are more particularly interested in the so-called "tuberculous heart," which expresses how tuberculous infection, localized in some particular structure, especially affects the cardio-vascular apparatus.

The tuberculous heart is characterized by three signs, namely, by tachycardia, microcardia and hypotension. These signs may differ in degree and are not determined by pulmonary localization of the infection. They may favour or promote it, but they are not secondary to changes in the haematosic field. They are the consequence of ***tuberculous impregnation***. I wish especially to stress the significance of hypotension, for Potain and Teissier considered it very useful for differentiating true forms of chlorosis not affecting blood pressure from the chlorotic conditions symptomatic of tuberculosis.

The presence of tuberculosis should naturally not be judged solely from the presence of hypotension, but the facility with which the latter may be measured, under ordinary clinical conditions, constitutes it a clinical test which should be applied to all doubtful cases, all cases of irido-cyclitis, for example, not presenting convincing reasons for being considered syphilitic. I am fully aware that hypotension occurs frequently, especially in young people, and that it is nearly constantly present in certain non-tuberculous affections, such as typhoid or para-typhoid, or infection with b. coli. I do not claim at all that it is a ***pathognomonic sign, but that it is a necessary sign***. In the presence of irido-cyclitis of doubtful nature, the origin is probably not tuberculous if hypotension is absent. Here probability must be largely allowed for. Just as essential glaucoma never occurs during phthisis, blood pressure is never high in tuberculosis save in the presence of nephritic conditions, of special type. These diagnostic elements are independent of rules. They are more particularly derived from ***custom***, and the latter formulates the law in pathology, as in other sciences.

(*c*) Humoral signs.—The fact that ocular tuberculosis proves to be secondary tuberculosis renders it difficult from the viewpoint of aetiological diagnosis, to utilize the data accumulated on this point as a result of biological studies. Attempts to utilize them in

ophthalmology should be respected. They are numerous, and, just as I was writing that the Vernes reaction proves useful in ophthalmology, my colleague Lacroix, of Rouen, was publishing an article presenting a large number of facts. When the humoral test proves the presence of tuberculosis, however, the aetiological diagnosis of the ocular lesion is not established. Is not the occurrence of a cuti-reaction positive to tuberculin entirely a normal sign?

III.—The Method of Choice

However, should all of this work be discarded? Are so many attempts wholly vain? Extreme pessimism should be avoided. Three special methods appear already to be highly promising, as follows:—

1. Tuberculin diagnosis, applied according to the given case either in the form of ***test treatment*** or in the form of the ***homeotopic technique*** of Marc Weiss.

2. Micro-leucocytic culture, as employed by Löwenstein.

3. Search for the ultra-virus of tuberculosis by the intraglandular inoculation of guinea pigs.

Tuberculin diagnosis, in cases presenting reactions positive to tuberculin, may supply absolutely decisive findings referable to focal reactions (at the affected site) in the course of test treatment with tuberculin. In cases in which the reaction is negative, the homeotopic method of Marc Weiss may give qualitative indications (according to the expression of Werdenberg) concerning the allergic condition present. When the reaction becomes negative, the reaction should be tested at the original site. If the patient is not sensitized to tuberculin, he is not tuberculous. If he becomes sensitized after a long time, his reactivity is low, and in other words, his immunity is diminished.

No conclusions are warranted from the work by Löwenstein, of Vienna. This work presents intensely interesting cases referring to the frequency with which the tubercle bacillus may be found in the blood during various diseases, but these studies are as yet incomplete and it is not yet practicable to define the field of so-called "emergent" tubercle bacilli or the pathogenic significance of such bacilli.

Search for the tuberculous ultra-virus seems to merit attention on account of recent work on tuberculous rheumatism suggested by the labours of Antonin Poncet and also on account of the facility with which, by simple puncture of the anterior chamber of the eye, it is possible to make aetiological verification by inoculating the glands of guinea pigs.

IV.—The Morphological Diagnosis of Irido-ciliary Tuberculosis

At the site of the irido-ciliary diaphragm, the characters peculiar to the development of tuberculosis are naturally associated with signs supplied by the anatomy and physiology of the special structures which are affected. These include a reservoir containing differentiated fluids, in mysterious equilibrium, and a muscular diaphragm of delicate texture, designed for adaptation and accommodation. These peculiarities determine special signs which are independent of the specificity of the infecting bacterium. Here tuberculosis develops in a mesenchymatous system. Whether productive or exudative, it is bathed by the interstitial liquid and develops amid muscular fibres and glandular structures. In short, it finds, on a narrow surface, the structural elements favourable to the production of lesions which may also occur in the pleura, serous membranes of the joints, or the pulmonary or glandular tissue, but never occur in such a variety in such a tiny space in any other part of the organism.

The wide variety of the clinical forms of irido-ciliary tuberculosis is quite familiar. The reporter has not been requested to describe these forms and he naturally limits his work to the production of an outline which may be easily filled from the copious data readily available. In completing the task with which he has been honoured, he has naturally sought to present clearly established points. There can be no disagreement with the thought that strict and close analysis is essential in any work of value and that all unknown quantities should be excluded from discussion.

The masters in medicine who lived during the epoch-making work of Pasteur and the discoveries of Villemin and Robert Koch have accomplished their tasks. They completed clinical and bacteriological investigations. They have perfected descriptions and created methods of examination tending to establish the specific characters possessed by various diseases. Whatever the anatomico-clinical form assumed by irido-ciliary tuberculosis, the lesions which we have studied result from a number of different factors. Some of these refer to the bacillus and others to conditions of the local tissues. Clinical facts, experimental findings and studies in allergy show that even an identical specific substance (bacillary or tuberculous products) capable of releasing a reaction produces in different tuberculous individuals, or in the same individual at different periods of his disease, reactions which are different. This fact already suffices to explain in large measure the variety of pathological reactions which may occur.

But Bordet pointed out, at the International Tuberculosis Conference held at the Hague, in 1932, that a positive cuti-reaction

may be obtained with a tuberculous organism by means of a filtrate of b. coli, which is entirely identical with the reaction produced by tuberculin in the same organism. Bezançon notes in his address given at the Twenty-second French Congress on Medicine that the substance extracted from a culture-free glycerinated bouillon gives a cutaneous reaction with tuberculous individuals which is analogous with that produced by tuberculin. A tuberculous individual may thus react identically either to specific substances, such as tuberculin, or to non-specific substances, such as a b. coli filtrate or even an extract of a culture-free glycerinated bouillon. Such data show most strikingly how complex is the idea of specificity.

V.—Conclusion

A study of the diagnostic methods which I have examined thus indicates certain rules of procedure, but uncertainties still remain and must persist until there is fuller information concerning the reciprocal influences of diatheses, hereditary dystrophies, congenital infectious diseases and acquired infections. Venneman frankly admitted inability to determine the part played by gout, tuberculosis and hereditary syphilis in the persistent form of iritis observed by Hutchinson in children born of gouty parents. Such questions are not solved as yet. In the general problem concerning morbid specificity, the question of associated affections, such as scrofula and syphilis, requires explanation.

When these problems become clear, and when clinical work shall be completed by knowledge of the pathogenic conditions which are still obscure in irido-ciliary tuberculosis, we shall render due respect to the pleas which have been faithfully made in directing attention to the frequency of tuberculous irido-cyclitis. In this department of tuberculosis, in which the truth develops only incompletely and in a fragmentary way, and in which observed facts supply no complete solutions, it is as yet too soon to generalize. Much, however, has been accomplished in obtaining so many useful data and in finding the direction which studies and research should take.

ANNOTATION

The Rôle of Filtration in the Maintenance of the Intra-ocular Pressure

In the forward march of any scientific work with its penetration and conquest of new fields, its changing direction of advance and the varying phases of its encounters, it is at times desirable for the participants to stand apart and review in panorama the ground over

which progress has been made, and to sift and assess the accumulated evidence of experimental facts before consolidating the position up to date.

Sir John Parsons in a paper published in the *Quarterly Journal of Physiology*, Vol. XXIII—a number dedicated to Sir Edward Sharpey-Schafer by his past and present assistants in honour of his eighty-third year—on "The rôle of filtration in the maintenance of intra-ocular pressure" has taken a long and wide view of the debated problems concerning the production and drainage of the intra-ocular fluid.

His judgments on the various theories that have come to the front from time to time are impartial, balanced and tempered with the wisdom that comes of long laboratory and clinical experience. The paper contains a brief survey of the early researches of Leber and Starling, who maintained that the intra-ocular fluid was formed by a simple process of filtration. Sir John Parsons's experiments at University College in 1902-3 led him to believe that the facts were not inconsistent with a process of simple filtration though it seemed to him improbable that the living capillary wall would behave in so simple a manner. The selective transmission of immune bodies and the excess of chlorides in the intra-ocular fluid as compared with the blood plasma were facts hostile to the filtration theory. In more recent years the brilliant biophysical and biochemical researches of Duke-Elder have shown that the intra-ocular fluid is a dialysate from blood plasma and all the experimental facts support the theory of a thermo-dynamical equilibrium between the blood and intra-ocular fluid.

Sir John Parsons comments that though these biophysical and biochemical reactions must now be admitted as fundamental to the process of lymph formation they are explanatory of only static conditions and that the rôle of filtration still plays an important part. The intra-ocular pressure is never static but follows passively the normal changes in blood pressure due to pulse and respiration, and the activities of the extrinsic ocular muscles and the lids.

The mechanical blockage of the filtration angle in secondary glaucoma affords evidence of the importance of the filtration of fluid out of the eye through the canal of Schlemm.

The author says that "neither dialysation nor filtration, nor both together, suffice to explain all the facts of normal and abnormal intra-ocular pressure. The dialysation theory has to fall back upon the variable permeability of the capillary walls in the various tissues of the body to explain the differences of lymph-pressure and constitution; and this variable permeability is at present only explicable on teleological grounds."

ABSTRACTS

I.—RETINA

(1) **McAlpine, Douglas (London). — Hypertensive retinitis.** *Lancet*, November 26, 1932.

(1) The reviewer has read **McAlpine's** article with care and has come reluctantly to the conclusion that he is not capable of reducing it to the form of an abstract which would not be apt to mislead the reader through what would be merely a partial statement of the author's closely reasoned argument. The thesis, based partly on the work of others and partly on his own, is that the terms "albuminuric," or "renal" retinitis, should be given up and replaced by the term "hypertensive." The matter may be summed up in the author's words: "The term 'hypertensive' should replace that of 'albuminuric' or 'renal,' as suggested by Fischberg and Oppenheimer, because the retinal changes, usually described under these names, may occur in the absence of any appreciable renal disease. Moreover, evidence is accumulating in favour of the view that, in certain cases of hypertension with albuminuria, the kidney is merely sharing in the effects of a widespread arteriolar constriction, the results of which may also be apparent in the fundus, brain, heart, and extremities." For the arguments the reader must go to the original.

ERNEST THOMSON.

(2) **Kalt, M. E. (Paris).—Exudative retinitis without vascular changes. (Rétinite exsudative sans altérations vasculaires).** *Ann. d'Ocul.*, Vol. CLXVII, p. 919, 1930.

(2) **Kalt** reports in detail the pathological findings in an eye of a woman, aged 73 years, affected with exudative retinitis in the macular and perimacular area. Beyond the fact that after enucleation a white appearance like a halo was seen around the macular area of the divided eye, nothing was known of the fundus oculi owing to the presence of cataract. Kalt refers to four clinical cases of exudative retinitis in patients with no evidence of retinal vascular disease. He cites these as examples of the same type as that of the case examined histologically. These cases all fall into what is called "the second or chronic (*torpide*) group of albuminuric retinitis," in which at the time of examination no albuminuria may be found. The first group is that of "acute albuminuric retinitis," of cases seen commonly at hospital

including those of pregnancy, with swollen optic disc, macular star and haemorrhages. In the case examined by serial sections no trace of disease of blood-vessels—even of the capillaries—could be found with careful search. It is suggested that the exudate, which consists of structureless coagulated albumen in the sections is the result of toxins which, entering by way of the optic nerve, increase the permeability of the capillaries. The exudates all occur in the inner nuclear, the internuclear and to a less extent the outer nuclear layers—the site of the smallest blood-vessels. The intensely swollen disc with exudates and haemorrhages in cerebral tumour cases are compared with the changes of acute albuminuric retinitis of eclampsia, and the simple oedema of tumour cases with the appearance of chronic albuminuric retinitis. In the eclampsia cases it is well recognized that the eye changes are due to a toxic effect on the capillaries and in the severe changes of cerebral tumour a similar cause may obtain. The toxins are presumed to reach the eye from the meninges by way of the subdural space and thence through the optic nerve to the retina at the posterior pole of the eye. For this to occur, it is assumed that toxic products of renal disease, capable of producing meningeal oedema are present in the cerebro-spinal fluid.

For details of the histological appearances—with illustrations—and of the white retinal exudates with rare haemorrhages and occasional glistening crystals in the four clinical cases, the original paper should be consulted.

HUMPHREY NEAME.

(3) **Bessière, E. (Bordeaux).—Does diabetic retinitis occur in the absence of renal disease? (Existe-t-il une rétinite diabétique en l'absence d'altérations rénales?)** *Arch. d'Ophtal.*, April, 1932.

(3) In a research into the question indicated in the title of this paper, **Bessière** has made a careful examination of 23 diabetic subjects with ocular lesions. In a very long communication, he culls from the writings of many previous observers, as far back as Jaeger in 1858. He gives clinical notes of 18 cases under his own observation, with two coloured drawings of sections of the retina from a case of glycosuria and albuminuria. He then discusses the question at issue in the light of the views of earlier observers and the findings in his own patients. He holds that though "this question demands further study" diabetic and albuminuric retinal lesions are analogous. "The appearance of retinitis in a non-albuminuric diabetic should be considered as a premonitory sign of approaching renal insufficiency." "Every

diabetic the subject of an exudative retinitis, is in reality, an undiscovered renal case." To this paper is appended a very full bibliography containing 84 references.

J. B. LAWFORD.

(4) **Goulden, Charles (London).—Spontaneous and traumatic detachment of the retina and its modern treatment.** *The Irish Jl. of Med. Science*, Series 6, No. 84, p. 679, December, 1932.

(4) **Goulden** in the Montgomery Memorial Lecture, delivered at the Royal College of Surgeons in Ireland on November 25, 1932, gave a description of the development of the human retina, the history and theories concerning the aetiology of retinal detachment from the time of its recognition early in the last century to the present day. The manner in which a retinal tear occurs is discussed and statistics are given concerning its incidence, site, and clinical variety. Stress is laid on the importance of taking a careful case history of the local symptoms, visual disturbances, "floaters," "phosphenes," and the part of the visual field first affected. The object of this is to obtain some idea of the site of the retinal tear which often corresponds to the part irritated so as to produce a "phosphene" and to the area of retina first detached. Methods of examination and the technique of localization of retinal tears are described. Brief accounts of Gonin's operation, Guist's caustic operation and the operation by diathermy are given. Tables of operative results terminate the paper.

H. B. STALLARD.

(5) **Arruga, H. (Barcelona).—Considerations on the cure of detached retina. (Consideraciones sobre la curacion del desprendimiento de la retina).** *Arch. de Oftal. Hisp.-Amer.*, Vol. XXXII, 381, p. 461, September, 1932.

(5) **Arruga** describes in detail, with clinical notes, typical case histories from a group of 38 patients with cured detachment. Altogether 158 cases were operated on of which 38 remained cured for intervals varying from two months to three years and eleven months. A large number of the patients were myopes and in all cases save three, the hole was found. The operation performed varied. In the group of successful cases puncture with the thermo-cautery was used twice, with the galvano-cautery 24 times, while the Lindner-Guist operation and a modification of it were also employed. The duration of the detachment before operation varied from two days to a year. Restoration of visual acuity was not complete in the majority of cases, but many showed pre-existing choroido-retinitis.

IDA MANN.

II.—THERAPEUTICS

(1) **Jahnke, W. and Wámoscher, L.—Serumtherapy in pneumococcal affections of the eye. (Zur Frage der Serumtherapie bei Pneumokokkenerkrankungen des Auges).** *Zeitschr. f. Augenheilk.*, Vol. LXXIV, p. 215, 1931.

(1) **Jahnke** and **Wámoscher** review the literature on the type of pneumococcus found in pneumococcal eye conditions. Out of 85 cases reported by different authors, 71 showed pneumococcus Type IV. Of 73 cases investigated by the authors, 51 were likewise of this type. Only one case in their series belonged to Type I. Seeing that serumtherapy is effective only in Type I, it holds out but little hope in the treatment of pneumococcal conditions of the eye.

ARNOLD SORSBY.

(2) **Aulamo, R.—Treatment of ocular tuberculosis by X-rays. (Ueber Röntgenbehandlung bei Augentuberkulose).** *Acta Ophthal.*, Vol. X, p. 159, 1933.

(2) **Aulamo** reports on 160 cases of ocular conditions diagnosed as tuberculous and treated by X-rays. Twenty-three were cases of phlyctenular disease and the remainder, cases of iritis, iridocyclitis, scleritis and choroiditis and allied conditions. One to five applications had to be given, and in one case seven; 79 per cent. of phlyctenular conditions were cured as also 91 per cent. of iritis cases, and 82 per cent. of uveitis cases, whilst of the remaining conditions, cure was obtained in about 60 per cent. of cases. The treatment is simple and without danger when used with care; the poorest results are in sclero-keratitis, choroiditis and iridocyclitis.

ARNOLD SORSBY.

(3) **Ferrer, Horacio.—Treatment of ocular tuberculosis by guaiacol sulphate and calcium. (Tratamento de la tuberculosis oftalmica con el sulfonata de guayacol y calcio).** *Arch. de Oftal. Hisp.-Amer.*, Vol. XXXIII, No. 7, p. 367, July, 1932.

(3) **Ferrer** states that he became impressed with the dangers of too great a focal reaction during the treatment of ocular tuberculosis with tuberculin, even the most minute doses being followed occasionally by grave consequences. He therefore attempted to find some substitute or adjuvant, and after having tried and abandoned phototherapy as uncertain in action, he began in 1923 to experiment with guaiacol sulphonate and calcium. He uses a 10 c.c. injection twice a week at the beginning and works up

gradually to three injections a week of 20 c.c. each. Case notes of ten patients are given in detail. The patients ranged from 15 to 35 years. In more than half there were proved tuberculous lesions elsewhere (phthisis, lupus, etc.). All were treated with intravenous guaiacol sulphonate and calcium as adjuvant to local treatment with atropine and heat. In some cases generalized ultra-violet light also was given. All the cases cleared up with good visual results in time varying from one to six months. Some of them have been under observation since 1927 and have remained well until the present time.

IDA MANN.

(4) **Bordas.—The use of percaine in ocular therapeutics. (El uso de la percáina en terapeutica oftalmológica).** *Arch. de Oftal. Hisp. Amer.*, Vol. XXXII, No. 11, p. 596, November, 1932.

(4) This paper deals with **Bordas'** experiences in the use of percaine as a substitute for cocaine. He concludes that it is equally efficacious as an anaesthetic and possesses certain advantages and also disadvantages. In the first place it produces anaesthesia in much weaker dilutions than cocaine, namely, 0.5 per cent. or even 0.1 per cent. It also possesses the advantage of being thermostable and can be sterilized by boiling. It is non-toxic and exercises no harmful effect whatever on the corneal epithelium. It may cause some conjunctival hyperaemia but this can be abolished by one drop of adrenaline. On the other hand, full anaesthesia is not produced for 15 to 30 minutes and the patients often complain of much irritation and burning when it is instilled. This can be avoided by beginning with very weak solutions. As in other local anaesthetics its action is much weakened in the presence of acute inflammation. It forms a useful substitute for cocaine when required over a long period, as in superficial keratitis, but its use is somewhat limited.

IDA MANN.

(5) **Weekers, L. (Liège).—The treatment of spasmodic entropion by injection of alcohol into the eyelid, associated with canthotomy. (Traitement de l'entropion spasmodique par l'injection palpébrale d'alcool associée à la canthotomie).** *Arch. d'Ophtal.*, July, 1932.

(5) Some five years ago **Weekers** reported a series of cases of spasmodic entropion successfully treated by injection of alcohol into the lid. Some of his patients remain cured after more than five years, but in others the entropion has become re-established. Weekers now adds canthotomy to the treatment by injection and has obtained more satisfactory results. His technique is, in brief,

the subcutaneous injection of 1 c.cm. of a 4 per cent. solution of novocaine, along the length of the palpebral border of the eyelid and in the region of the external canthus: canthotomy with straight scissors: injection of 1 to 1.5 c.cm. of 80 per cent. alcohol under the skin of the lid. To avoid necrosis of the epidermis the injection should penetrate deeply. The treatment is painless and does not necessitate detention of the patient. Seven cases have been thus treated; the longest period is 1½ years; no relapses have been noted. In one instance the effect was rather excessive.

J. B. LAWFORD.

III.—MISCELLANEOUS

(1) **Bishop Harman (London). — Minor Surgery of the eye.** *Medical Press and Circular Supplement*, February 1, 1933.

(1) A new feature in the weekly issue of the Medical Press and Circular is the quarterly supplement on minor surgery for the benefit of those in general practice. The first supplement contains short accounts on the minor surgery of the eye, the foot, the ear, and muscles and tendons.

It goes without saying that the section on the eye by **Bishop Harman** is well done. He deals with certain features of the treatment of conjunctival conditions, the methods of removal of foreign bodies from the cornea and conjunctival sac, the operative treatment of chalazion, some forms of corneal ulcer, and the examination of the lacrymal apparatus with the treatment of lacrymal abscess. A competent general practitioner should be able to deal with any of these conditions and thus save the patient hours of discomfort and actual pain. The in-growing lash or the cilium that has been washed into the lower or upper canaliculus is easily overlooked and nearly always easily to be removed. The author strikes a timely note of warning when he says that though he has described these small operations as minor, there is nothing little about them. Each may be almost as serious as an acute glaucoma; each if neglected may destroy an eye.

R.R.J.

(2) **Copeland, M. M. and Hayes, M. E. (New York City) — Xeroderma pigmentosum.** *Amer. Jl. of Cancer*, Vol. XVI, No. 6, 1932.

(2) Xeroderma Pigmentosum, or Kaposi's disease is a rare condition marked by roughening, dryness, pigmentation, and ulceration of the skin; it is often accompanied by the formation

of telangiectases and tumours in the skin. Its course is prolonged but invariably fatal and eye changes have been reported by several observers in this country, notably by Richardson Cross. Copeland and **Hayes** report four cases. The first occurred in a Jewess, aged 22 years. She was the offspring of healthy parents who were first cousins, and at birth she was normal in all respects. She was one of a family of four children, the others being healthy. The first signs of Kaposi's disease showed themselves when she was two years old and followed exposure to sunlight. There was at first generalized redness of the skin which later was transformed into brownish spots like freckles. The skin became dry and scaly and pigmentation increased. At the age of 8 years she had treatment by radium for the keratoses in the region of the face and was then lost sight of. At last loss of vision in the left eye brought her back to hospital. She was then found to be fairly well nourished, the hair was normal, the skin of the face showed irregular, deeply pigmented areas interspersed with areas of leukoderma. Keratoses were present abundantly, especially in the area of the outer canthus, and there was a papilloma of the right upper lid. The right eye showed an irregular nodular mass invading the nasal half of the cornea; the lower lid showed ectropion; in spite of a previous operation to correct it. The left eye was normal. The nose was much deformed. Because of inflammation of the right eyeball, the globe was excised and at the same time a small warty mass was removed from the right temple; the latter proved, on microscopical examination, to be a pigmented basal-celled epithelioma.

The second case occurred in an Italian girl of nine years of age in 1930. The disease first appeared at the age of eighteen months and had steadily progressed, the cornea having been ulcerated. When admitted to hospital she was found to be in fair bodily health with no marked anaemia. The skin of the face was much involved by dry, scaly patches with marked pigmentation, ulceration and fissures. From the edge of the right upper lid a polypoid ulcerating mass protruded. The cornea showed extensive leucomata. Treatment by radium produced a temporary improvement. In 1928, the left eyelids showed extensive ulceration. Biopsies showed plasmo-celled granulomata. The orbit and left antrum became involved. The patient died early in 1930.

The other two cases occurred in sisters, aged 6 and 5 years respectively. The general signs were well marked and in addition conjunctivitis and ectropion were present. A biopsy taken from the neck of the elder girl showed a squamous-celled carcinoma, grade I. A later biopsy showed that the carcinoma was then of grade II, radio-resistant. She was in much the same state in April, 1932, and no further notes of her case are available.

The younger sister, also an Italian, began to show signs of the disease at nine months. On admission, in 1930, extensive ulceration was present at the angle of the mouth; a biopsy of this ulcerated area showed the presence of squamous-celled carcinoma, grade I, radio-resistant. The general condition has remained fairly satisfactory.

In commenting on these four cases the authors say that consanguinity appears to be a factor in the case, though whether heredity plays any rôle, is a debatable point. Not all the members of a family need be affected. A good description of the pathological lesions is followed by a careful analysis of the aetiological factors. The exciting cause would appear to be exposure to the actinic rays of the sun in cases which are predisposed to the condition. There may be a relationship between Kaposi's disease and haematoporphyrinuria though in congenital haematoporphyrinuria xeroderma does not occur. In two of the author's cases examination of the urine was negative, and the blood of one of them showed no laking. The disease is invariably fatal, death usually occurring before the twenty-first year of life. The treatment is for the most part palliative: parents are advised to keep the sufferers in doors as much as possible, and when out of doors those parts of the body exposed to sunlight should be suitably protected by black clothing, shades, gloves, etc. In early cases radium therapy seems to be beneficial, but is not indicated if the lesions are wide spread.

The article is illustrated by excellent photographs of the children's faces, and microphotographs of the biopsies. A bibliography of 33 items completes the paper. Richardson Cross's paper in the *Ophthalmic Review*, Vol. XXXIV, 1915, occupies a place, but the authors have missed his paper in the *Trans. Ophthal. Soc. U.K.*, Vol. XXXV, and the pathological report by Affleck Greeves in the same volume.

R.R.J.

(3) **Gourfein Welt, Madame L. (Geneva).—Haemorrhagic form of sympathetic ophthalmitis. (Ophtalmie sympathique forme hémorrhagique).** *Rev. gen. d'Ophtal.*, June, 1931-2.

(3) This fully reported case by **Gourfein Welt** is one which must have caused great difficulty in diagnosis and prognosis especially as to the question of excision. Briefly, the patient was a boy, aged 8 years, who was wounded seriously in the right eye by the explosion of a detonator. Radiography failed to disclose any foreign body and the eye quickly quieted down. The patient was dismissed from hospital in a fortnight. Two months later he returned with a profuse haemorrhage in the right anterior chamber

which absorbed and recurred several times. Exactly two months later again there was a vitreous haemorrhage in the left eye with a soft-looking disc (*papille floue*) and slight dilatation of the veins on the disc. Visual acuity 5/10. The right eye was now removed: it was injected, soft and sightless. The left vitreous cleared up; the eye became normal with full visual acuity. On dissection, the right eye was disorganized and it contained a small piece of copper which radiography had failed to reveal. Full details of the personal and the family history and of the examination of the excised eye are given by the author, who concludes as follows:—

"The case is one of sympathetic ophthalmitis in the very rare form which affects the posterior segment of the eye, sympathetic papillitis. Influenced by this, ocular haemorrhages occurred due to a pre-existing defect, namely, the blood instability diathesis known as haemogenesis (*hémogenie*)."

ERNEST THOMSON.

(4) **Saradindu, Sanyal.—Fungus infection of the eye.** *Calcutta Medical Journal*, Vol. XXVII, No. 6, December, 1932.

(4) **Sanyal** begins this paper with a brief review of the types of fungus infection found in the lids, canaliculi, conjunctiva, and cornea of human beings. He describes a case of a married Hindu female, aged 15 years, suffering from ptosis due to a thickened upper lid on the conjunctival surface of which were reddish finger-like projections. The palpebral conjunctiva of the lower lid was uneven but smooth and covered by a yellowish-red mass. At operation the mass on the palpebral conjunctiva was found to be friable and contained numerous granules. It was removed by curetting. Pathological examination revealed a streptothrix. Recovery was complete in ten days.

H. B. STALLARD.

(5) **Panico (Rome).—Paradoxical pupil reaction. (Reazione paradossa della pupilla).** *Rass. Ital. d'Ottal.*, September-October, 1932.

(5) The paradoxical reaction of the pupil to light is rare, but the paradoxical reaction to accommodation is much rarer. The first is almost always preceded by miosis, and is always associated with severe syphilitic lesions of the central nervous system. There are several conditions which may give rise to the diagnosis of paradoxical reaction to light, when this is not really present: of these the most common depends on the fact that the eye under examination may diverge either from muscular paresis or heterophoria; we may then often see movement of the pupil.

HAROLD GRIMSDALE.

(6) **Tonelli, Lanfranco (Italy).—Deformation of the pupil as a sign of death.** *Policlinico*, February 8, 1932.

(6) The problem of distinguishing with absolute certainty between real and apparent death is one that has given physicians concern since the earliest times. Many people have a fear of being buried alive although the physician who gives the death certificate has numerous methods of determining that life is extinct. Tonelli's paper is referred to at length in the *American Medical Journal* for October 29, 1932. Here only the ocular signs of death will be referred to. A dilated pupil with a film on the cornea is usually taken to be a fatal sign, though it is certainly not a sure one. If the subject is examined ophthalmoscopically a few minutes after death the capillary redness of the optic disc disappears, and its surface becomes very pale. The arteries cease to be recognizable upon the disc, appearing to commence at its edge, beyond which they are at first distinct. The columns of blood in the vessels soon become interrupted and broken into segments, giving a beaded appearance. The arteries become unrecognizable, while the veins remain distinct with increased beading. The normal tint of the choroid lessens in intensity. The retina commences to become opaque, while there may be a red spot at the macula similar to that seen in embolism of the central artery. These appearances persist until, after some hours, the progressive opacity of the media prevents further observation. These observations were made by Sir William Gowers.

The injection of fluorescein into the circulation of a living creature quickly results in staining of the conjunctiva. This experiment must obviously fail in a corpse. It is pathognomonic of death.

According to Tonelli strong pressure applied with the two fingers to the eyeball of a living or apparently dead person produces nò modification of the round contour of the pupil. However, in a corpse bilateral pressure applied to the eye, even though slight, will produce an easily observable deformation of the pupil, which becomes oval, triangular or polygonal, depending on the direction of the force applied. The research was carried out in 649 cases.

A. F. MACCALLAN.

(7) **Oswaldo (Padua). — The variation of visual acuity with diminishing light. (Sull' acutezza visiva a luce decrescente).** *Ann. di Ottal.*, September, 1932.

(7) In the observations which have been made on the subject of the variation of visual acuity in diminishing light, no account has been taken, says Oswaldo, of the size of the pupil. He has tested the acuity of a number of individuals both with the normal

pupil and with the pupil dilated by homatropine. The dilatation of the pupil has two effects: by enlargement it allows a greater amount of light to enter the eye but at the same time by uncovering the periphery of the lens a greater degree of blurring of the image is found owing to aberration. In the tests Oswaldo used a Landolt's ring 1·5 mm. broad. This was placed at 6 m. from the patient and illuminated by a lamp whose power was varied by a resistance between 41·5 candles (Hefner) and 0·035 candles. The acuity in the undilated eyes showed little decrease until the light had fallen to one-tenth of the maximum. From this point onward the acuity fell rapidly. With the dilated pupil the acuity diminished more rapidly, but below a certain intensity, the two curves were very close. The curve of variations of acuity with the undilated pupil is approximately a hyperbola.

HAROLD GRIMSDALE.

(8) **Bardanzellu (Genoa).—A note on the study of oxycephaly. (Contributo clinico allo studio dell'oxicefalia).** *Arch. di Ottal.*, May, 1932.

(8) The term "oxycephaly" has been used in two senses: to indicate a form of skull, and also to indicate a form of pathological closure of the cranial sutures, bringing about changes in the base of the skull and in the optic nerves, without necessarily gross deformity of the general shape of the skull. There has been great difference of opinion as to the place of synostosis causing the oxycephaly. Virchow thought that the fault lay in the premature closure of the sutures between the occipital and the adjacent parietal and temporal bones. Most other observers founding their opinions on radiographs, think it due to closure of the sagittal and coronal sutures. In the case which **Bardanzellu** narrates a premature synostosis (lordosis basilare) was accompanied by atrophy of both optic nerves, marked exophthalmos with spontaneous luxation of the left eye, and nystagmus. The boy showed signs of rickets, but as Bardanzellu points out, this could not have any bearing on the oxycephaly.

HAROLD GRIMSDALE.

(9) **Alajmo (Catania). On the importance of the colour fields for the diagnosis of lesions of the chiasma. (Sull'importaza del campo visivo dei colori per la diagnosi di "Sindrome chiasmatica").** *Rass. Ital. d'Ottal.*, September-October, 1932.

(9) **Alajmo** reports a case in which the examination of the colour-fields in the only eye with vision led to the discovery of a pituitary tumour. The administration of X-rays was followed by considerable recovery of the eye previously blind, but the better eye failed.

HAROLD GRIMSDALE.

BOOK NOTICES

Entwicklung der Augenheilkunde im 18 und 19. Jahrhundert mit besonderer Berücksichtigung der Schweiz. VON DR. ALFRED BADER. 231 pages with 34 illustrations, 10 facsimiles and 3 tables. Basel: Benno Schwabe and Co. 1933. Price, 8 Swiss francs, unbound; 10 francs, bound.

Friedrich Horner died in 1886 at the age of 55. He thus lived through the tumultuous days of the fifties and sixties of the last century, when modern ophthalmology was born. No doubt he felt, as Wordsworth did on another occasion, that bliss it was in those days to have been alive, but to have been young was very heaven. He settled in Zürich in 1856 as "a maid of all work," as he himself explained, and was appointed to the chair in ophthalmology in 1862. In the subsequent 24 years he laid the basis for the distinguished position Swiss ophthalmology holds to-day. A loveable man and a distinguished oculist he was fortunate in his friends, counting most of the great figures of the ophthalmic world amongst them. He must have been a good correspondent, for though his own letters have been lost, 160 addressed to him have been collected and are published in the present volume. These letters covering the period from 1855 till 1886 contain invaluable correspondence from von Graefe, Donders, Bowman, von Helmholtz, Duke Carl Theodor, von Hippel, His, Krönlein, Snellen and others. Much more than any formal history do they convey the thrill of those years. Inevitably there is much that is of purely personal interest, but the personal affairs of giants are matters of public interest. An authentic note of the humility of a great man is struck by Donders in a letter accompanying a presentation copy of his newly published "On the anomalies of refraction and accommodation": "Il contient à peu près tout ce que j'ai fait dans les 5 dernières années, ce qui est bien peu de chose pour un si grand lapse de temps." Other letters are crowded with news from all parts of the continent of the strange doings that were going on in ophthalmic clinics, what with the ophthalmoscope, von Graefe's new fangled operations for glaucoma and linear extraction of cataract and with Lister's antisepsis. But the letters are equally important documents on the social history of ophthalmology, for the difficulties and struggles of ophthalmologists against the overbearing surgical departments which still regarded ophthalmology as part of their domains are frequent subjects of discussion.

The author has rendered a service by publishing these letters and we must join him in regretting that Horner's replies to his correspondence have been lost. The full correspondence would have been as charming as it would have been valuable.

Dr. Bader introduces the correspondence by an interesting essay of 82 pages on the development of ophthalmology during the 18th and 19th century. He stresses in particular the obstructionist attitude of the surgical clinics in the struggle of ophthalmology for independence during the first half of the nineteenth century. Some interesting sidelights on Swiss ophthalmic history are also brought out.

CORRESPONDENCE

OCULAR CONDITIONS IN DIABETES MELLITUS

To the Editors of THE BRITISH JOURNAL OF OPHTHALMOLOGY.

SIRS,—I have read with great interest Dr. Gray's paper on Ocular Conditions in Diabetes Mellitus and I hasten to congratulate him on the wealth of material, the minute and careful examination, and on the result achieved. As a fellow worker in the same field, may I be allowed to make some remarks?

In spite of the tremendous advance of the Insulin Era, the real aetiology of Diabetes Mellitus is, in my opinion, still unknown. One important factor is missing, that of the disturbance of cellular metabolism. As pointed out by Dr. Gray and many other writers, this disorder of cell metabolism would explain the fact that in many cases the retinal exudate is not accompanied ophthalmoscopically by degeneration of the retinal vessels. The predominance of capillary degeneration is sufficient to explain the peculiarities of diabetic exudates and haemorrhages. The same, or perhaps another missing factor, eventually produces, as a rule, an arterial hypertension. It is seldom as pronounced, or as advanced as in essential hyperpiesis and correspondingly the sclerosis of the retinal vessels is not so marked. In diabetes the sclerosis of retinal vessels is a phase intermediate between senile and hyperpietic changes. Neither Dr. Gray nor myself have yet seen diabetic retinitis in young persons or children.

I should like to make some criticism on the following three points in this important paper.

1. Historically, Marcus Gunn was the first to describe sclerotic retinal vessels and, although Dr. Gray follows Gunn's enumeration of symptoms, he omits to mention a remark of the utmost importance: "That the loss of translucency is the first and earliest pathological change." After Gunn, chronologically follows, not Foster Moore (much as I admire his work), but Röelman and particularly Hertel.

2. Some mistakes, probably printer's errors, have been made in the tables. All figures of retinal arterial pressure are printed in reverse order, *i.e.*, diastolic instead of systolic pressure and *vice versa*.

3. It is rather a pity that in cases of changes in the peripheral

vessels (presumably of the lower limbs) with gangrene, no oscillometric measurement was done. If the oscillometric index were normal as near to the affected part as possible, probably the gangrene would be due to capillary degeneration. If the index were minute or there was no movement of the needle at all, it would mean obliteration of the main arterial branch. These particulars would be of special importance, as Gray rightly states, in the absence of any definite retinal vascular sclerosis. A point always difficult to decide is the distinction between a congenital and a pathological anomaly. This especially applies to arterio-venous compression in its protean forms. With certain technical means this difficulty, in my opinion, might be overcome if the observer paid special attention to the very fine white lines accompanying the artery and crossing the vein at the point of intersection of both vessels. These white lines increase with the degree of vascular degeneration and are best seen in the "hour glass" compression of the vein. Gray mentions that Gunn first described them. Quite so, but only in normal vessels. (Adams Frost describes this also.) As an important pathological sign they were not described, as far as I know, until 1929.

The translucency of the retinal vessels is of such a delicate quality that it may sometimes disappear within a few hours, as from any infectious disease, such as, severe tonsillitis. Therefore one cannot say that in diabetes there is a "loss of translucency and perhaps some cutting of one of the lesser veins by the super-imposed artery." This is seen in 99 per cent. middle-aged normal people. This is why one sometimes wonders what is meant when in clinical histories some fundi are described as "normal," in which case the translucency of the retinal vessels should still be present. The description of arteries as "somewhat straighter than normal," especially in patients with high blood pressure, seems to me rather unusual, as the description of all other writers points rather to increased tortuosity. Magitot-Bailliart's ingenious method is not easy to master. Dr. Gray has certainly mastered it to perfection, but he states that the first pulsations indicate diastolic pressure. It would take us too far to go fully into retinal arterial pressure, but the first pulsation probably indicates not the diastolic, but the mean pressure. Lately, Magitot expressed this opinion also. Measurements of mean brachial pressure are completely absent in Gray's paper.

In 36 cases declared to be hyperpietics the systolic blood pressure alone is noted. The term "intra-ocular pressure," as measured by Schiötz tonometer, instead of "tension" is probably a *lapsus linguae*, because "pressure" can be measured only by the method of Magitot and Bailliart.

Yours faithfully,

N. PINES.

NOTES

Indicia Ophthalmologica

THE second edition of this valuable list of the ophthalmic surgeons of the world has been published. Copies may be obtained from the Editor, Eduard Ijdo, Hooglandsche Kerkgracht, 4, Leiden. The price is 7 Swiss francs.

* * * *

North of England Ophthalmological Society

THE annual lectures, which are a feature of the meetings of the North of England Ophthalmological Society, will be given by Dr. Harald Gjessing, of Drammen, Norway. Dates and subjects are as follows:—

At the University, Manchester, on January 5, 1934, at 4.30, on "The value of eye symptoms in the diagnosis of internal disease."

At the University, Sheffield, on January 8, at 4.30, on "The value of the ophthalmic symptoms in the diagnosis and localization of brain tumours."

At the County Hospital, York, on January 9, at 4.30, on "The importance of the previous history and the spontaneous remarks of the patient in the diagnosis of diseases of the eye."

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Appointments

MR. L. P. JAMESON EVANS, M.A., M.B., B.Ch.Cantab., has been appointed Assistant Surgeon to the Birmingham and Midland Eye Hospital.

Dr. J. López Lacarrère has been appointed chief of the ophthalmic clinic of the Hospital of the Infant Jesus at Madrid.

FUTURE ARRANGEMENTS

1933

November 10.—Section of Ophthalmology, Royal Society of Medicine.

November 17.—North of England Ophthalmological Society, at Bradford.

December 5.—Midland Ophthalmological Society, at Birmingham and Midland Eye Hospital.

December 8.—Section of Ophthalmology, Royal Society of Medicine. (Clinical Meeting.)

December 15.—North of England Ophthalmological Society, at Leeds.

1934

January 12.—Section of Ophthalmology, Royal Society of Medicine.
February 9.—Section of Ophthalmology, Royal Society of Medicine.
February 16.—North of England Ophthalmological Society, at Newcastle-on-Tyne.
March 9.—Section of Ophthalmology, Royal Society of Medicine. (Clinical Meeting.)
March 16.—North of England Ophthalmological Society, at Liverpool.
April 13.—North of England Ophthalmological Society, at Sheffield.
May 11.—Joint Meeting of the Midland and North of England Ophthalmological Societies, at Nottingham.
June 8.—Section of Ophthalmology, Royal Society of Medicine. (Annual.)

CONTEMPORARY OPHTHALMIC LITERATURE

American Journal of Ophthalmology. *September, 1933.*

WASSENAAR. Angioid streaks of the fundus oculi.
JACKSON. The history of cataract operations.
OHMART. Experimental tuberculosis of the eye.
BERENS and SITCHEVSKA. Complete discission of the crystalline lens.
McD. VAN POOLE. A new stitch in cataract operation.
TOWN. Cyst of the uveal layer of the iris.
LEVINE. Growth of corneal epithelium into anterior chamber.
MARSHALL. Cerebral pseudotumours or chronic arachnoiditis.
WILLIAMS. A possible explanation of one type of colour blindness.

Archives of Ophthalmology. *September, 1933.*

VOGT. Operative treatment of detachment of the retina.
KNAPP. Operative treatment of chronic glaucoma; report of two hundred successive operations.
KLAUDER. Ocular syphilis: IV. Interstitial keratitis and trauma; clinical, experimental and medico-legal aspects.
SLOCUM and ARBOR. Employment of conjunctival bridge and suture in cataract extraction.
HEATH. Ocular lipid histiocytosis and allied storage phenomena.
BERLINER. Herpes corneae occurring after artificial hyperpyrexia induced by diathermy.
BURKY. Relation of ocular sensitivity to the arthus phenomenon in the rabbit.
KUZNETSKAYA. Trachoma: treatment with chaulmoogra oil.

Annales d'Oculistique. *September, 1933.*

REDSLOB. On the pathogenesis of expulsive haemorrhage.
VALIÈRE-VIALEIX. A case of pulsating exophthalmos treated and cured by ligature of the orbital veins at the entrance to the orbit. Considerations on the treatment. Glaucoma in exophthalmos.

ADIAMANTIADIS. Ocular complications of acne rosacea.
LAZARESCU, D. and LAZARESCU, E. Neurogenous heterochromia of the iris and syndrome of Claude-Bernard-Horner. Clinical observations and experimental researches.
NICOLAU. Contribution to the study of the first epidemic of acute dacryo-adenitis.
PAVIA. Cinematograph of the fundus of the eye.

Archives d'Ophtalmologie. *September, 1933.*

COPPEZ, H. On the conditions in retinal detachment when operative measures must be realised.
COPPEZ, L. The use of the pyrometric electrode in the treatment of retinal detachment.
RUBBRECHT. The suture in retinal detachment.
TERRIEN. The adjuvant factors in interstitial keratitis.
VIALLEFONT. The ocular manifestations of sympathetic posterior cervical syndrome.

Revue d'Optique. *June-July, 1933.*

DUNOYER and PAOUNOFF. On the "second order" of function of certain photo-electric cells in a gaseous atmosphere.

Klinische Monatsblätter für Augenheilkunde. *September, 1933.*

ENGELKING. Gonin or Weve?
MACHEMER. Contribution to the physiology and pathology of the pupil.
BRAAK and VAN HERWAARDEN. Ophthalmo-encephalo-myelitis.
KAYSER. Anatomy of eyes with megalocornea.
POOS. The general efficacy of pharmacotherapy in ophthalmology.
SCHNEIDER. Cataract extraction in a haemophiliac.
ENGELKING. Scheme for noting down the process of dark adaptation.
BAHR. Sight and vegetative neurosis.
KOCH. On the varying retention of corneal tattooing in growing and adult rabbits.
TÓTH. X-ray investigation of the lacrymal ducts.
FAZAKAS. On double lacrymal canaliculus and epiphora.
LUSZA. The blood picture of the trachomatous patient.
PAVIA. Technique and result of cinematography of the fundus oculi.

Annali di Ottalmologia e Clinica Oculistica. *May, 1933.*

GIANNINI. Clinical contribution to the study of familial amaurotic idiocy and the analogous hereditary degenerative form. (*Continuation and end.*)
KOCH and BRUNETTI. Study of the morphological connection between orbital and bulbar dimensions in the living with the help of a new system of radiographical orbital measurement (with special attention to anisometropia and to unilateral anophthalmos).
BIFFIS. Influence of the aspherical surface of the lens on the spherical aberrations of the eye.

Archivio di Ottalmologia. *May, 1933.*

VELE. Paracentesis of the anterior chamber and the injection of atropine to 0/00 as a therapeutic co-adjutant in optic atrophy.
SPINELLI. Congenital pseudo-papillary stasis.
FERRARI. Keratoconus and familial degenerative internal otitis. Oculo-auricular syndrome.

Bollettino d'Oculistica. *August, 1933.*

NICOLATO. On the possible causes of a deep anterior chamber in primary glaucoma.
TROVATI. Functional retinal reserve (Trovati) in abridged binocular field of vision, and in panoramic monocular field of vision.
DE-PETRI. Sarcoma of the choroid and glaucoma.
VELE. On tumours of the eyelids. (Clinical and histopathological study.)
HESKY. Clinical contribution to changes in the eye derived from intra-ocular aluminium particles

Lettura Oftalmologica. *February, 1933.*

ADDARIO LA FERLA. On the aetiology of papillary stasis, and on its importance in the diagnosis of endocranial affections with considerations on the semeiological and pathogenetic treatment from the examination of 52 cases.
SANGUINETTI. Remarks on corneal ulcers of reapers.

March, 1933.

GARAU. Research on the development of conjunctivitis in relation to the time of year, and to the bacteriological findings.
VELE. Trachoma in the city, and in the province of Parma during the twelve years, 1921-1932.

April, 1933.

PERGOLA. On cystic tumours of the conjunctiva.
ADDARIO LA FERLA. On the efficacy of Elliot's scleral trephine with iridectomy in the cure of serious ulceration of the cornea.
VELE. Further contribution to the study of corneo-conjunctival teratomata.

August, 1933.

ALIQUÒ-MAZZI. Cataract and myotonia atrophica.
BARDANZELLU. Spasm of the orbicularis in the pathogenesis of certain clinical forms of entropion and ectropion.

September, 1933.

CROCI. Contribution to the knowledge of pseudo-diphtheritic conjunctivitis.
BUSACCA. Operations for secondary cataract.
ROI. The varying behaviour of the gonococcus in ophthalmia neonatorum.

Archivos de Oftalmologia Hispano-Americanos. *September, 1933.*

LUQUE. Arterio-venous crossings and thrombosis of the retinal veins.
BARRENECHEA. Inflammatory glaucoma without permanent raised tension.
KAPLAN. Acute ocular neuro-myelitis.
VERDAGUER. Two years' experience of Gonin's operation for retinal detachment.

Anales de la Sociedad Mexicana de Oftalmologia y Oto-Rino-Laringologia. *July to December, 1932.*

FERRER. Treatment of ocular tuberculosis with sulphonate of guaiacol and calcium.
VÉLEZ. The chromoptometer and the measure of refractive defects of the eye.
ALONSO. Traumatic lesion of the cortical centre of vision. Anatomico-physiological considerations.